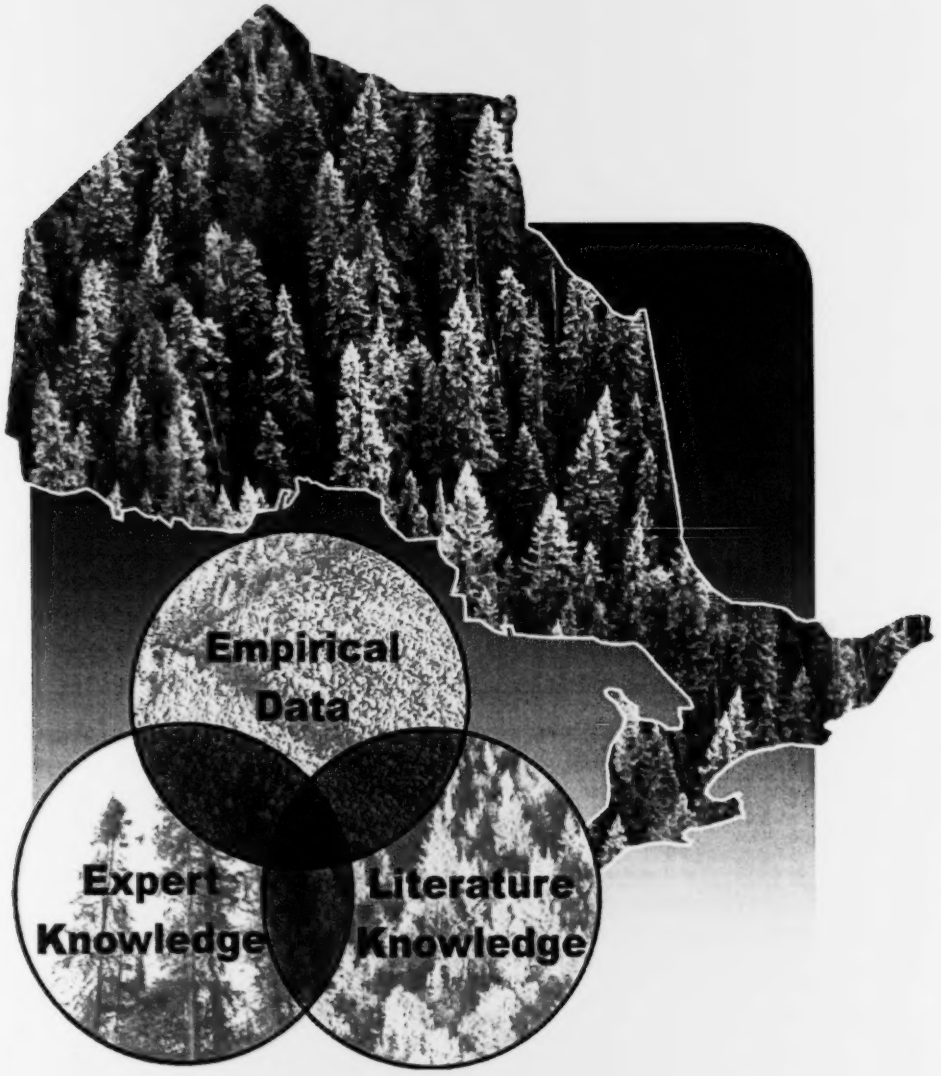
Forest Research Report No. **171**

Boreal forest succession in Ontario: an analysis of the knowledge space



Ontario

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Forest Research Report No. 171

Boreal forest succession in Ontario: an analysis of the knowledge space

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2008

APPLIED RESEARCH AND DEVELOPMENT • ONTARIO MINISTRY OF NATURAL RESOURCES

Library and Archives Canada Cataloguing in Publication Data

Main entry under title:
Boreal forest succession in Ontario : an analysis of the knowledge space [electronic resource]

(Forest research report; no. 171)
Includes bibliographical references.
Electronic monograph in PDF format.
Mode of access: World Wide Web.
Issued also in printed form.
ISBN 978-1-4249-7872-4

1. Forest regeneration—Ontario. 2. Forest dynamics—Ontario. 3. Taiga ecology—Ontario.
I. Drescher, M. II. Ontario Forest Research Institute. III. Series: Forest research report (Online) ; no. 171.

SD409 B67 2008 634.9'5609713 C2009-964006-6

© 2008, Queen's Printer for Ontario
Printed in Ontario, Canada

Single copies of this publication are available from:

Ontario Forest Research Institute
Ministry of Natural Resources
1235 Queen Street East
Sault Ste. Marie, ON
Canada P6A 2E5

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Fax: (705) 946-2030
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Abstract

Reliable knowledge of forest succession is vital for successfully designing management strategies leading towards desired future forest states. At present two main sources of knowledge of forest succession are used: experienced practitioners (experts) and published research studies (literature). The contents of these two sources may overlap, but their interactions are implicit and fuzzy and the choice of which is used in forest management applications appears often arbitrary. Hitherto, no rigorous efforts have been made to explore these two knowledge sources for their respective strengths and weaknesses or to examine their concordance and possibilities for integration. The broad goal of the work reported here was to explore the body of boreal forest succession knowledge, to elucidate its strengths, weaknesses, and gaps, and to quantify its levels of uncertainty.

We first elicited expert knowledge and its uncertainty using information from expert workshops and compilations of expert knowledge, followed by a review of published knowledge and an estimate of its uncertainty. The two sets of knowledge were compared to identify general areas of high and low knowledge availability, and analyzed to discern areas of concordance and discordance. Subsequently, we statistically compared both knowledge sets to an independent empirical data set of boreal of forest cover change to assess their agreement with empirical data. The results indicated that expert knowledge of boreal forest succession is extensive, but contains a high degree of uncertainty in some aspects. For example, effects of mesic site conditions on forest succession and the generalized patterns of succession in species-rich forest types appeared to be less known than succession under extreme site conditions and immediately post-fire. Published knowledge is abundant for simple forest types and pioneer species, such as jack pine, relative to, for example, lowland coniferous forests. Overall, knowledge of the effects of site conditions on succession and the patterns of succession in species-rich mixed forests is sparse. Knowledge of natural succession from the two sources was most congruent in southeast boreal Ontario, and least in northwest boreal Ontario. Published knowledge revealed similarities in natural succession patterns among ecogeographical regions despite differences in succession postulated by expert knowledge.

To augment the present body of knowledge, we identify three key areas for research: forest succession following non-stand replacing disturbances, especially in late successional forests; effects of site conditions on post-fire establishment; and succession dynamics in mixed forests. These research studies must be rigorous, and focus on testing hypotheses formulated from both published and expert knowledge. We also recommend placing concerted effort on quantifying the currently qualitative and descriptive knowledge to facilitate its use in simulation models and decision support systems that have become increasingly popular as management tools. These efforts must consider the need to spatially scale up stand level knowledge to the landscape level, as well as infusing the stochasticity and variability inherent to forest succession, to match the broadening scales of forest management planning.

Acknowledgements

We thank three anonymous reviewers whose comments on an earlier version of the report improved its clarity and readability.

Résumé

Une connaissance fiable en matière de succession des forêts est cruciale afin de mettre en place des stratégies de gestion réussies qui permettront d'atteindre l'état des forêts voulu à l'avenir. Pour l'instant, nous puisons dans deux principales sources de connaissance en matière de succession des forêts : les spécialistes d'expérience (experts) et les études techniques publiées (littérature). Il peut y avoir chevauchement du contenu de ces deux sources, mais leurs interactions sont implicites et imprécises et le choix de celles-ci quant aux applications en matière de gestion forestière est souvent arbitraire. Aucun effort rigoureux n'a été fait jusqu'ici pour explorer ces deux sources de connaissance en fonction de leurs forces et de leurs faiblesses respectives ou pour examiner leur concordance et leurs possibilités en vue d'intégration. L'objectif général du travail mentionné ici visait à explorer l'ensemble des connaissances en matière de succession en forêt boréale, de dégager ses forces, faiblesses et lacunes ainsi que de quantifier ses degrés d'incertitude.

Nous avons examiné le degré d'incertitude sur le plan de la connaissance experte en utilisant les renseignements provenant des ateliers d'experts et des compilations de la connaissance d'experts. Nous avons par la suite examiné la littérature et nous avons tenté de découvrir les sources de cette incertitude. Les deux ensembles de connaissances ont été comparés afin de définir les zones générales où on dispose de connaissances approfondies ou non et ils ont été analysés afin de discerner les zones de concordance et de discordance. Par la suite, nous avons procédé à une comparaison statistique des deux ensembles de connaissances à un ensemble indépendant de données empiriques de changement du couvert forestier boréal afin d'évaluer la qualité de ces ensembles. Les résultats ont confirmé une connaissance d'experts approfondie en matière de succession des forêts boréales, malgré le fait que certains aspects de cette connaissance comportent un degré d'incertitude élevé. Par exemple, les effets des conditions de site mésique sur la succession des forêts et les modèles généralisés de succession au sein des types de forêt comportant une diversité d'espèces semblaient moins connus que la succession lorsque le site est soumis à des conditions extrêmes et immédiatement après un incendie. La connaissance publiée est exhaustive lorsqu'il s'agit de types de forêts simples et d'espèces pionnières, comme le pin gris, en comparaison, par exemple, de la connaissance liée aux forêts de conifères des basses terres. En général, la connaissance des effets des conditions du site sur la succession et les modèles de succession dans les forêts mixtes comportant une diversité d'espèces est éparse. La connaissance de la succession naturelle des deux sources était plus harmonisée dans les forêts boréales du sud-est de l'Ontario que dans celles du nord-ouest. La littérature a révélé des similitudes dans les modèles de succession naturelle au sein des régions écogéographiques malgré les différences dans la succession posées en principe par la connaissance d'experts.

Pour approfondir l'ensemble actuel de connaissances, nous avons défini trois principales zones de recherche : la succession des forêts à la suite de perturbations de remplacement autre que du peuplement, particulièrement dans les forêts de succession tardives; les effets des conditions du site pour l'établissement d'espèces à la suite d'un incendie et la dynamique de la succession dans les forêts mixtes. Ces études techniques doivent être rigoureuses et se concentrer sur la vérification des hypothèses qui ont été formulées par les experts et celles trouvées dans la littérature. Nous recommandons également de déployer un effort concerté pour quantifier la connaissance qualitative et descriptive actuelle afin d'en simplifier l'utilisation dans les modèles de simulation et les systèmes de soutien à la prise de décision qui sont de plus en plus populaires en tant qu'outils de gestion. Ces efforts doivent prendre en considération le besoin d'augmenter spatialement la connaissance au niveau du peuplement ainsi que de connaître les sources de stochasticité et de variabilité propres à la succession des forêts pour faire correspondre les échelles étendues de la planification de la gestion forestière.

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Introduction

Forest succession can be viewed, from a tree-centric point of view, as the temporal pattern of changes in tree species composition that occur following a disturbance that destroyed the existing forest cover, and includes the initial re-establishment of the forest cover. Fire is one such natural disturbance in boreal forests (Payette 1992). The typically large and intense fires destroy much of the pre-existing forest cover and organic soil layer, initiating a new sequence of secondary succession. Depending on the season of burn, tree seedlings and sprouts can reestablish in the year of the fire, though most develop over a period of up to ten years (Johnstone et al. 2004). This period is referred to as the post-fire establishment or stand initiation phase. The composition of this first cohort of regeneration depends mainly on the species composition of the pre-existing forest cover. During this phase, establishment strategies vary with species: from an aerial bank of serotinous seeds that typically survive fires or sprouts and suckers that can re-vegetate, both providing an in situ source of propagules, to seed dispersed from outside the burned areas. Additionally, abiotic factors such as soil water and nutrient availability can affect site suitability for seedling establishment and influence species composition.

After the post-fire establishment phase, many of the saplings may die due to competition for resources such as light and water. During this period, which is referred to as the stem exclusion phase, initial size differences among saplings become amplified as height growth of the taller saplings accelerates (Oliver and Larson 1990). These saplings suppress the smaller ones, eventually dominating the species composition of the forest canopy for several decades. The timing depends on factors such as tree species longevity, site conditions, and minor disturbances such as pests and pathogens.

Underneath the forest canopy, a sub-canopy of shade-tolerant trees may exist that established at about the same time as the dominant canopy trees but were suppressed because of initially lower growth rates. Or, delayed seeding may result in the establishment of a secondary cohort of shade-tolerant trees that persists in the understory as advance regeneration. In either case, species composition of the forest canopy changes only when dominant trees start decaying. When the forest canopy is a single species and even-aged, many trees can die within a short period resulting in a sudden change in canopy species composition as new trees grow from the sub-canopy or understory. When the species composition is diverse or uneven-aged, trees may die individually over a longer period, resulting in an extended period of mixing, before the previous sub-canopy or advance regeneration dominates the forest canopy.

With increasing time after fire, the life phases of individual trees are increasingly asynchronous because of individual variation in growth rates and mortality. Individual tree deaths and small canopy gaps may therefore become more frequent, allowing individual trees of mostly shade-tolerant species to grow into the canopy. Small disturbances or those of low to intermediate severity, such as insect pests or wind, may create larger canopy gaps and temporarily allow re-establishment of some light-demanding species. In general, however, shade-tolerant tree species are more likely to dominate the canopy. Such forests are often referred to as old-growth forests and are considered to be in dynamic equilibrium in terms of structure and species composition: over smaller scales diversity in structure and/or species composition exist but over larger scales this diversity decreases.

These changes in species composition may be interrupted at any time by a new wildfire that destroys the forest stand. The removal of the previous forest cover leads to the re-establishment of a new forest stand and another cycle of forest succession is initiated.

Use of boreal forest succession knowledge in forest management

Understanding the temporal patterns of changes in tree species composition of forests is referred to as knowledge of forest succession. This knowledge is essential to understand possible future forest states in relation to their present states. It is also fundamental for developing plans to successfully guide tree species composition towards desired future forest states through forest management.

Provincial habitat guidelines, such as those for pileated woodpecker (*Dryocopus pileatus*) (Naylor et al. 1996), marten (*Martes americana*) (Watt et al. 1996), and white-tailed deer (*Odocoileus virginianus*) Voigt et al. 1997), emphasize the essential function of managing for specific forest composition and structure to provide suitable habitat for wildlife. As well, policy documents such as the wilderness policy (OMNR 1997), old growth policy (OMNR 2003), and forest management planning manual (OMNR 2004a) give explicit direction for preserving natural dynamics of forest composition and structure. Successful application of these directions depends on thorough understanding of the patterns and processes of boreal forest succession.

Examples of the use of forest succession knowledge in forest management can also be found elsewhere in North America. For example, McNay et al. (2005, 2006) used forest succession knowledge in modelling timber supply and mountain caribou (*Rangifer tarandus*) habitat in British Columbia. Keane et al. (2006) used knowledge of forest succession in the western United States in a model of forest landscape dynamics to compare outcomes resulting from alternative forest management plans. And, Herbert (2003) used knowledge about forest succession to evaluate the sustainability of various harvesting techniques in the boreal mixed forests of Quebec.

Given the extensive use of forest succession knowledge in quantitative tools applied for the purposes of forest management planning and evaluation, this knowledge should be explicit, quantitative, and abundant. However, the adequacy of the available forest succession knowledge for boreal Ontario has been questioned. For example, the provincial wood supply strategy (OMNR 2004b) as well as participants of a recent forestry workshop on timber supply (Sobze et al. 2006) identified the importance of improved knowledge of forest succession for predicting future wood supply in Ontario.

Nature of boreal forest succession knowledge sources

The two main sources of boreal forest succession knowledge are expert opinion and the published scientific literature (Charnley et al. 2007).

Expert knowledge is held by practitioners with many years of experience. Their knowledge is usually not formalized or quantified and therefore remains largely subjective (Ford and Sterman 1998). Expert knowledge results from a combination of practical experience and discussion with other experts (Charnley et al. 2007), but may include insight gained from formal education and/or a study of the relevant literature. Typically, practical experiences that are the basis of expert knowledge are founded on personal observations of forest dynamics at small spatio-temporal scales while the processes that give rise to forest succession operate at a variety of scales. The validity of extrapolating expert knowledge, which may be very precise, beyond the scale of the original observations is uncertain (Chalmers and Fabricius 2007). Therefore, expert knowledge can be viewed as a form of abductive reasoning that is useful for generating new hypotheses about forest succession.

Scientific studies of the pattern and processes of forest succession have been published for more than a century. Typically reported are the quantitative results of observational or experimental research but conceptual studies of forest succession also exist. Study scales vary widely, ranging from the micro-site (Simard et al. 1998) to continental (Meunier et al. 2007), but the stand level is most common. Observational or experimental results from such studies can be used to generate new hypotheses about

boreal forest succession for research, but practitioners remain faced with a major challenge in scaling of individual tree or forest stand observations to the forest management-relevant landscape and regional scales. When gathered in a suitable sampling design, the results can also be used in an inductive way for falsification of hypotheses about forest succession.

Knowledge from expert opinion, the scientific literature, or some combination of both may be used as input for quantitative tools applied in forest management. However, the latter approach works only when knowledge from both sources agree or complement one another, particularly for knowledge gaps, which may occur for the entire knowledge space covered by both sources or only portions of it. If they differ, some way of combining both sources has to be devised or one of the sources selected. The choice of knowledge source could be based on the level of credibility of each source. However, the widespread use of knowledge from both experts and the scientific literature indicates that both knowledge sources are often considered equally credible (Charnley et al. 2007). Therefore, selecting a source for application should be based on the availability of relevant knowledge, its strength of evidence (e.g., data, observations, or inference; cf. Failing et al. 2007), and level of uncertainty.

Despite the dilemma of having to choose among knowledge sources, the extent that each is used, the rationale for choosing one over another, or the methods used to combine both sources are usually not explicit (e.g., Hemstrom et al. 2007, Keane et al. 2006). To date, no rigorous attempts to quantify the level of agreement between knowledge from experts and that from the published literature are documented. Nor have these knowledge sources been investigated for their strength of evidence or levels of uncertainty. It is therefore unclear whether the choice of knowledge source is a problem and, if so, its seriousness. In fact, many practitioners are either unaware of the dilemma or lack information that would help them select between sources. This hampers their ability to make well-informed decisions about which knowledge source to use when developing forest management policies and practices.

Goals and objectives

We developed a research study to investigate and test knowledge of forest succession following stand-replacing wildfires in boreal Ontario that was derived from expert opinion and the published scientific literature. Our goal was to improve the overall knowledge space. The study consisted of three main phases: (i) eliciting knowledge from expert opinion and from the literature and investigating its uncertainty, (ii) deriving quantitative hypotheses/models from expert and published knowledge and investigating the level of agreement between sources, and (iii) testing the quantitative hypotheses/models from expert and published knowledge against empirical data and determining the respective level of support from that evidence.

This report provides an overview of the results of the three main phases of the study, synthesizes those results into an improved overall space of boreal forest succession knowledge, and provides a basis for identifying boreal forest succession research needs. The specific objectives of this report are to:

(i) Describe the extent and uncertainty of expert knowledge

(ii) Describe the extent and uncertainty of published knowledge

(iii) Present explicit hypotheses/models based on expert and published knowledge and the results of testing those against empirical data

(iv) Synthesize information about the extent and uncertainty of expert and published knowledge and the results of the hypothesis testing into an improved overall knowledge space

(v) Recommend focus areas for future research based on uncertainties and gaps identified in the overall knowledge space.

Overall study methods

Study area ecogeography

With an area of almost 50 million ha, the boreal forest is Ontario's largest forest biome. It is largely dominated by coniferous tree species such as black spruce (*Picea mariana*), white spruce (*P. glauca*), balsam fir (*Abies balsamea*), and jack pine (*Pinus banksiana*), but locally pioneer broadleaf species, such as white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and balsam poplar (*P. balsamifera*), can dominate or be mixed with the conifers (OMNR 2002).

Within boreal Ontario, many experts differentiate ecogeographical regions (Figure 1) based on a system originally defined by Hills (1961) and subsequently refined (e.g., Burger 1993). All ecogeographical regions are underlain by the Precambrian rock of the Canadian Shield that gave rise to rocky landscapes interspersed with lakes and gently rising hills scattered with moraines, outwash channels, and lacustrine deposits left from Pleistocene deglaciation (Thurston 1991). Some ecogeographical regions differ slightly from this: ecoregion 3W3 is more varied with gently undulating sills mixed with steep hills and cliffs and the southeast of ecoregion 3E-Non claybelt is controlled by flat, sedimentary rock (Thurston 1991).

The climate of the study area ranges from subhumid to humid and from low boreal to high boreal (EWG 1989). Average summer temperatures range from 11.5°C to 15°C, average winter temperatures range from -9°C to -20°C, and average annual precipitation ranges from 400 mm to 1000 mm (ESWG 1995).

Figure 1. *Ecogeographical regions in boreal Ontario, as used by forest succession experts.*

Forest management hierarchy in boreal Ontario

Most forest area in Ontario is owned by the Crown and managed under forest licenses issued to forest industry. For administrative purposes, the province is divided into three regions (northwest, northeast, and southern) with forest management occurring in an area referred to as the area of the undertaking (or AOU), which consists of approximately 34.8 million hectares of productive, mainly boreal, forest. This area is divided into the northeast and northwest regions (Figure 2),

Regions are divided into districts, and further subdivided into forest management units that range in size from 0.24 million ha to 1.99 million ha. For each forest management unit, a management plan is developed for a 10-year period. In these plans, forest development (future forest states) is projected for 100 years using an aspatial model (for details see OMNR 2004a). Thus, forest management planning is applied at large spatial and long temporal scales.

In each administrative region, the information base used for forest management planning differs, for example, the ecoregional structure, the data sets (forest resource inventory, soil, etc), the cover type classification systems, and site type (geoenvironmental factors) definitions and categories all vary.

***Figure 2**. Ontario Ministry of Natural Resources' northwest and northeast administrative regions (shaded) and ecoregions (polygons) in Ontario. Heavy black line depicts boundary of the area of the undertaking (AOU).*

Forest cover types

Forest cover type information that is used in boreal forest management is derived from aerial photography, and subsequent manual interpretations and classifications. The forest resources inventory, based on air photos (1:15,840 and 1:20,000), classifies forest cover into broad compositional strings (e.g., Sb5Pj2Bw2Po1) that, in combination with site conditions and stand productivity, are further grouped into *standard forest units*. These standard forest unit classifications differ between Ontario Ministry of Natural Resources (OMNR) administrative regions as detailed in Ride et al. (2004) for northwest Ontario and Vasiliauskas et al. (2004) for northeast Ontario. In this study, we classified forest cover types into groups (*forest units*) that are largely parallel to the current regional standard forest unit classifications. We used forest units as described in Table 1 as initial states for forest succession.

Table 1. *Forest cover type classification system used in this study (forest units) compared to the classification system used by the Ontario Ministry of Natural Resources (standard forest units) in (a) northwest and (b) northeast Ontario. Note: Cover types with the same name may differ between regions.*

a. Northwest Ontario

Standard forest unit code	Forest unit code used in this study	Forest unit name	Forest unit definition*
PwDom	PW	White pine	Pw ≥40%
PrDom	PR	Red pine	Pr ≥70%
PrwMx	PRW	Mixed red and white pine	Pr + Pw ≥40%
OcLow	CONLO	Lowland conifer	(Ce + La ≥50% OR DG = Ce OR DG = La) AND Pr + Pw + Sw + Bw ≤10%
SbLow	SBLO	Black spruce bog	(Sb + Ce + La ≥100% AND SC = 3 OR 4) OR (Sb + Ce + La = 100% AND Ce + La ≥10% AND SC = 1 OR 2) OR (ES = ES35, ES36, OR ES37)
SbDom	SB	Black spruce	Sb ≥70% AND Po + Bw ≤20%
PjDom	PJ	Jack pine	Pj ≥70% AND Po + Bw ≤20%
PoDom	PO	Trembling aspen	Po ≥70%
BwDom	BW	White birch	Bw ≥60% AND Bw + Po ≥70%
OthHd	BRDOTH	Other broadleaf	Mh + Uh + Lh ≥30%
SbMx1	SBMX	Mixed black spruce	Pr + Sb + Pj + Sw + B ≥70% AND Bf ≤10% AND Po + Bw ≤20% AND (Sb + Sw) ≥ Pj
PjMx1	PJMX	Mixed jack pine	Pr + Sb + Pj + Sw + Bf ≥70% AND Bf ≤10% AND Po + Bw ≤20% AND Pj ≥ (Sb + Sw)
BfDom	BF	Balsam fir	Bf ≥30% AND Bf + Sw + Sb + Pj ≥ 50%
ConMx	CONMX	Mixed conifer	Pw + Pr + Sb + Sw+ Bf + Pj + Ce + La ≥50%
HrDom	BRD	Broadleaf	Po + Bw + Mh + Uh + Lh ≥70%
HrdMx	BRDMX	Mixed Broadleaf	Po + Bw + Mh + Uh + Lh ≥50%

* Bf – *Abies balsamea*; Bw – *Betula papyrifera*; Ce – *Thuja occidentalis*; La – *Larix laricina*; Lh – *Fraxinus nigra* and *Populus balsamifera*; Mh – *Acer* spp.; Pj – *Pinus banksiana*; Po – *Populus tremuloides.*; Pr – *Pinus resinosa*; Pw – *Pinus strobus*; Sb – *Picea mariana*; Sw – *Picea glauca*; Uh – *Betula alleghaniensis, Ulmus americana, Quercus* spp., and *Tilia americana*; ES – ecosite; SC – site class; DG – dominant group.

b. Northeast Ontario

Standard forest unit code	Forest unit code used in this study	Forest unit name	Forest unit definition*
PR1	PR	Red pine	Pr ≥70%
PW1	PW	White pine	Pw + Pr + Sw + He ≥40% AND Pw ≥30%
PRW	PRW	Mixed red and white pine	Pw + Pr ≥40%
LH1	BRDLO	Lowland broadleaf	Lh ≥30%
TH1	BRDTO	Shade tolerant broadleaf	Lh + Mh ≥ Uh ≥30%
SBOG	SBLOW	Black spruce bog	Sb + La ≥70% AND Pw = 0% AND SC = 4
SB1	SB	Black spruce	Sb ≥80% AND Mh + Uh + Pr = 0 AND Pw + Pj ≤10%
PJ1	PJ	Jack pine	Pj ≥70% AND Po + Bw + Uh + Mh + Lh ≤20%
LC1	CONLO	Lowland conifer	Sb + Ce + La ≥80% AND Mh + Uh + Pr = 0% AND Pw + Pj ≤10%
PJ2	PJSB	Mixed jack pine-black spruce	((Pj + Sb + Pr≥ 70%) OR (Pj≥ 50% AND Pj + Sb + Bf + Sw + He + Pw + Pr + Ce + La ≥70% AND Bf + Sw + He + Pw + Ce + La ≤20%)) AND Pj ≥ Sb
SP1	SBPJ	Mixed black spruce-jack pine	Sb + Sw + Bf + Ce + La + Pw + Pj + Pr + He ≥70% AND (Bf + Ce + Pw + La + Sw + He ≤20% OR Pj ≥30%)
SF1	CONMX	Mixed conifer	Sb + Sw + Bf + Ce + La + Pw + Pj + Pr + He ≥70%
PO1	PO	Trembling aspen	Po + Bw + Mh + Uh + Lh ≥70% AND Po ≥50%
BW1	BW	White birch	Po + Bw + Mh + Uh + Lh ≥70%
MW1	MWCON	Coniferous mixedwood	Pj + Pr ≥20%
MW2	MWBRD	Broadleaf mixedwood	All other species compositions

*Bf – *Abies balsamea*; Bw – *Betula papyrifera*; Ce – *Thuja occidentalis*; La – *Larix laricina*; Lh – *Fraxinus nigra*, *Populus balsamifera*, and *Acer rubrum*; Mh – *Acer saccharum*; Uh – *Betula alleghaniensis*, *Ulmus americana*, *Quercus* spp., *Tilia americana*; Pj – *Pinus banksiana*; Po – *Populus tremuloides*; Pr – *Pinus resinosa*; Pw – *Pinus strobus*; Sb – *Picea mariana*; Sw – *Picea glauca*; SC – site class.

Forest cover transition rules

Forest cover transition rules are attempts to quantitatively and explicitly formalize knowledge of forest succession processes for use in predicting future states of forest stands. Each transition rule describes one step in the transitional dynamics that lead to one forest type replacing another. For example, the transition rule for forest cover type A might describe the transition of a forest stand from forest cover type A to forest cover type B. Once the transition occurs, the stand is in forest cover type B and the transition rule for forest cover type B applies. The latter might describe the transition of a forest stand from forest cover type B to forest cover type C or D. Though every transition rule describes only one step in the transitional dynamics of forest stands, all transition rules together connect all forest cover types in a network of transition rules. The collective of all these transition rules is referred to as a transition rule set.

Each rule in a forest cover transition rule set contains three types of explicit information: definitions (composition and age) of the states of forest stands (present and future), definition of the time period between transitions, and the probabilities with which the transitions may occur. A hypothetical example (Figure 3) of forest cover transition for two distinct types of succession is:

(i) Post-fire establishment: A stand of forest cover type *A* replaces itself with probability f_{AA}, or is replaced by a stand of forest cover type *B* with probability f_{AB}, or by a stand of forest cover type *C* with probability f_{AC}.

(ii) Natural succession through time: A stand of forest cover type *A* replaces itself with probability s_{AA} is replaced by a stand of forest cover type *D* with probability s_{AD} after *u* years, or replaced by a stand of forest cover type *E* with probability s_{AE} after *v* years.

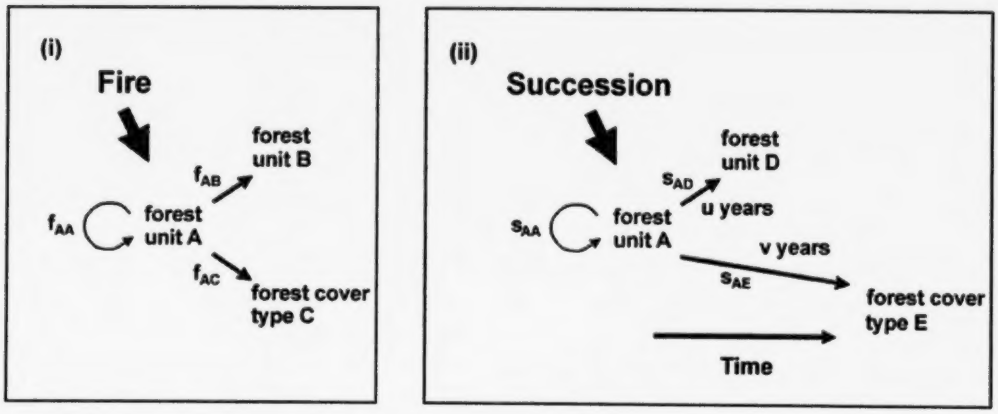


Figure 3. *An illustration of stand-level forest succession knowledge as explicit, quantitative rules describing forest cover transitions: (i) immediate forest cover establishment after fire – where f_{AA}, f_{AB} and f_{AC} denote probabilities of transitions, (ii) replacement of a forest stand by succession through time – where S_{AD} and S_{AE} denote probabilities of transition.*

For forest management purposes in Ontario, the forest cover transition rules used in planning are based on standard forest units (SFUs), and differ between northeast (Vasiliauskas et al. 2004) and northwest (Ride et al. 2004) regions. The knowledge base from which these forest stand transition rules are derived for the various spatial planning levels is mainly expert knowledge, unpublished observations, and reports. Forest stand transition rules for a few forest cover types, such as black spruce-dominated stands, have been specified at the level of the site condition to differentiate, for example, between dry upland and wet lowland sites (e.g., Ride et al. 2004). However, for most forest cover types, forest stand transition rules are not differentiated by site conditions, especially not for subtle differences, such as mesic versus wet soil moisture regime or mesotrophic versus rich soil nutrient regime. Though it is generally acknowledged that such variations in site conditions may affect successional dynamics, their effects have not yet been sufficiently quantified to generate evidence-based transition rules.

Final forest cover transition rules used in Ontario result from the consensus knowledge of regional forestry experts and are specified mostly at ecoregion, but sometimes at ecodistrict, resolution. Although these rules have been generalized and published as 'suggested rule sets', they are continually revised during local applications at the forest management unit level to reflect knowledge of local conditions.

Nature of expert knowledge of boreal forest succession

Expert opinion is an important source of forest succession knowledge. By elucidating expert opinion, this knowledge can be made explicit and quantitative and then integrated with the overall body of boreal forest succession knowledge. As well, its extent and relative level of uncertainty can be investigated. Here, we describe an exploration of expert knowledge of boreal forest succession. We detail how we assessed the extent of expert knowledge and its level of uncertainty using expert workshops, present the results of these assessments, and conclude by discussing the limitations of this component of the study.

Introduction

General characteristics of expert knowledge of boreal forest succession

Expert knowledge of forest succession, as we define it, is mainly held by experienced practitioners working as foresters, forest managers, biologists, or field ecologists in the public or private sector. For the most part, the extensive knowledge of these practitioners (hereafter called experts) is not explicit and formalized, i.e., it remains subjective, unquantified, and not well documented (Ford and Sterman 1998).

The origin of expert knowledge is usually a combination of practical experience and discussions with colleagues (Charnley et al. 2007) and is often mixed with formal education and familiarity with the literature. This expert knowledge may be acquired in a casual, unplanned way, driven by informal attempts (Leonard and Sensiper 1998) to understand forest succession. The range of practical experiences, which are essential to expert knowledge, is determined by the scale of personal observations. Many forest succession processes occur over spatial and temporal scales that do not match the scale of personal observations, often exceeding it, and vary spatially and temporally (Foster et al. 1998). Individual practical experiences therefore are not likely to supply information over the whole range of processes that determine forest succession, and the validity of extrapolations beyond the observed range is uncertain (Chalmers and Fabricius 2007).

Characteristics of this individual expert knowledge, such as its accuracy, resolution, or uncertainty, are usually only known by the individual expert (Bradley at al. 2000). In many cases, even the individual expert may not be familiar with these characteristics because the knowledge is implicit and seldom evaluated objectively (Leonard and Sensiper 1998). Since the overall body of expert knowledge, i.e., that held by a group of experts, comprises the knowledge of individuals, the characteristics of the overall body of expert knowledge (e.g., its accuracy, resolution, and uncertainty) are also unknown (Leonard and Sensiper 1998).

Importance of expert knowledge of boreal forest succession

The importance of expert knowledge of forest succession lies in its potential to fill the perceived gaps in the published information about forest succession. Consequently, many practitioners and researchers resort to the use of expert knowledge in many forest management and research applications.

Expert knowledge of boreal forest succession is used in various aspects of forest resource management. An example of its application in scoping and exploration is its use in combination with scientific data to improve understanding of effects of allowable cut in intensive forest management (Newton 2001). In strategic policy development it is used, for example, to project future forest landscapes in support of the development of the province's new landscape guide, scheduled for release in late 2008. Expert knowledge is also applied for the planning of forest management as exemplified by the succession rules input to the Strategic Forest Management Model (SFMM, Davies 1999), which is used for projecting and comparing future forest states resulting from different forest management scenarios. A final example of the application of expert knowledge is its tactical use for operational planning, such as in forecasting silvicultural needs including tending requirements for species composition management and competition control.

Uncertainty of expert knowledge

Uncertainty in the overall body of expert knowledge consists of two main components: First, the uncertainty of individual experts, *individual expert uncertainty*, and second, the uncertainty among individuals in a group of experts, *collective expert uncertainty*.

Individual expert uncertainty consists of two sub-components: (i) expert knowledge confidence and (ii) expert knowledge complexity (Drescher et al. 2008). Expert knowledge confidence is determined by the amount of information available about the process in question and can be increased by gathering more information. Expert knowledge confidence can also be referred to as epistemic or subjective uncertainty (e.g., Hora 1996). Expert knowledge complexity results from the inherent variability or unpredictability of the process in question and therefore is difficult to decrease. It can also be referred to as aleatory or random uncertainty (e.g., Hora 1996). Expert knowledge confidence and expert knowledge complexity combine to form individual expert knowledge uncertainty following an additive model where low confidence and high complexity lead to high uncertainty.

Collective expert uncertainty results from inter-expert variability of knowledge about the same process and has also been referred to as source conflict (Smithson 1999). Collective expert uncertainty is reduced when individual expert experiences overlap or when the variability of the process of interest is low.

Individual expert uncertainty and collective expert uncertainty combine to form the uncertainty in the overall expert knowledge body, hereafter referred to as *composite knowledge uncertainty*, following an additi model where high individual and collective uncertainty form high composite uncertainty.

Methods

Extent of expert knowledge of boreal forest succession

Exploring the entire body of expert knowledge of boreal forest succession would involve elicitation of the knowledge of all individual experts in Ontario. Alternatively, we can approximate that body of knowledge by eliciting knowledge from representative groups of experts.

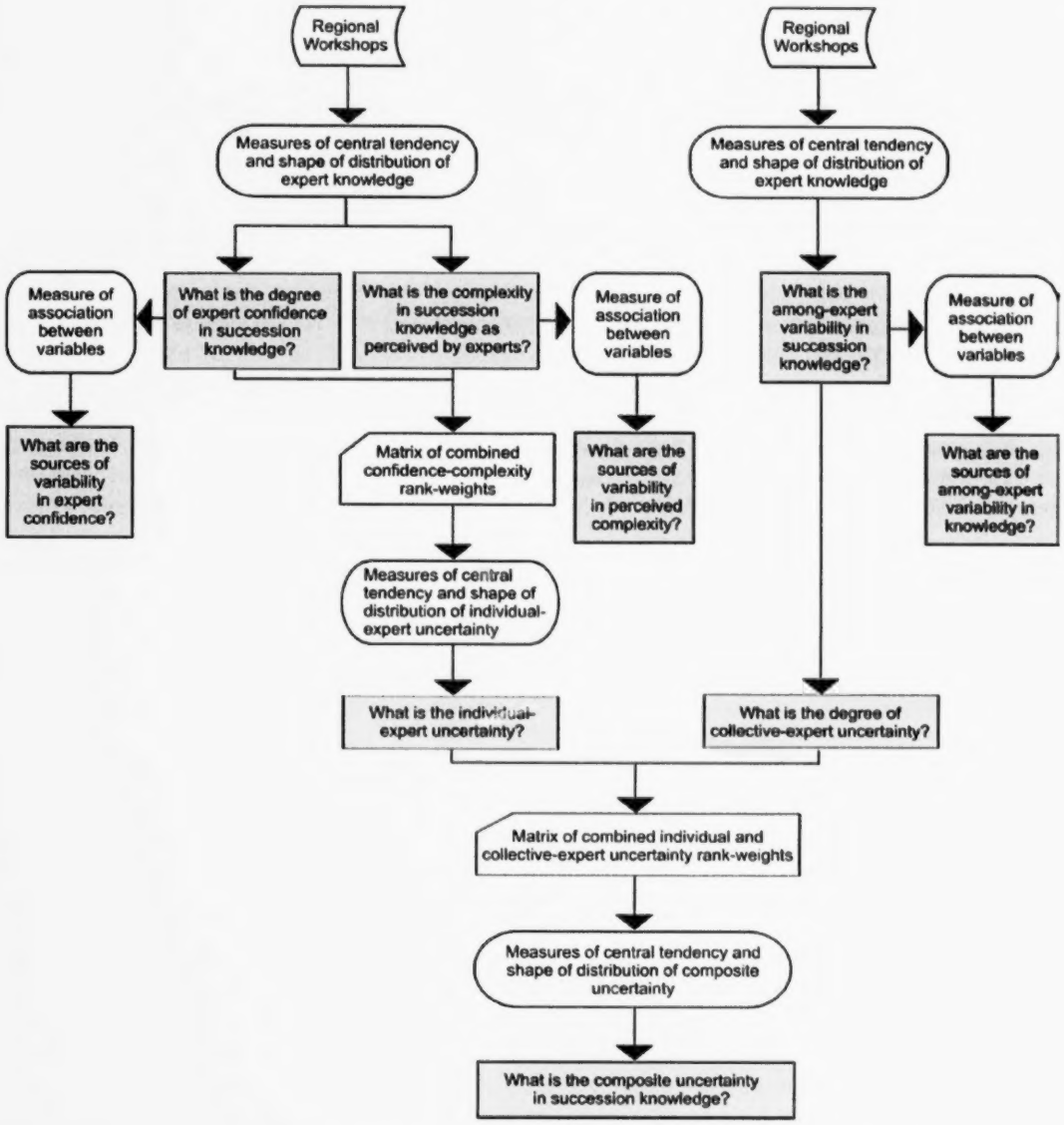
We based our exploration of the body of expert knowledge of boreal forest succession on two published reports of regional expert opinion about boreal forest succession that are considered compendia of expert knowledge (Ride et al. 2004, Vasiliauskas et al. 2004). In these reports, the authors present expert opinion about natural forest succession following stand-replacing wildfires for boreal Ontario. Expert opinions are expressed as landscape-level estimates of proportions of stands succeeding among forest cover types and presented as forest cover type transition rules. Since the reports do not discuss the effects of non-stand replacing disturbances on forest succession, it has to be assumed that these are considered integral to natural succession. Ride et al. (2004) present expert opinion about succession for ecogeographical regions in boreal northwest Ontario and Vasiliauskas et al. (2004) present expert opinion for ecogeographical regions in boreal northeast Ontario.

We used the information provided in these two reports to explore the extent of expert knowledge of boreal forest succession in terms of its geographical limits, ecological resolution (e.g., forest stand vs. forested landscape), spatial and temporal resolution and extent, and awareness of its stochastic nature.

Uncertainty of expert knowledge of boreal forest succession

We used forest cover transition rules provided in Ride et al. (2004) and Vasiliauskas et al. (2004) as a base to quantify expert uncertainty. These rules describe (i) the change in forest cover driven by wildfire from just before a mature forest stand is destroyed by fire to the end of the initiation phase of the new stand, referred to as *post-fire establishment* (only Ride et al. 2004) and (ii) the change of forest cover mainly driven by growth, mortality, and delayed establishment, starting after the stand initiation phase and continuing into the old-growth phase (cf. Oliver and Larson 1990) of the stand, referred to as *natural succession* (Ride et al. 2004, Vasiliauskas et al. 2004).

In a workshop setting, we asked experts to review the forest cover transition rules and adjust them if they felt it necessary. For each reviewed transition rule, experts assessed their knowledge confidence and knowledge complexity on a three-rank scale from low to high. The three-rank scale was used because it provides the most information when time is limited (Tversky 1964). We combined these values to quantify individual expert uncertainty. Further, we compared the reviewed transition rules among experts for their congruence, and used information about inter-expert variability to quantify collective knowledge uncertainty. We combined individual expert uncertainty with collective uncertainty to quantify composite uncertainty. An overview of this process is illustrated in Figure 4.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What is the complexity in succession knowledge as perceived by experts?
Measure of association between variables
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Figure 4. *An overview of the analytical approaches used in assessing uncertainty of expert knowledge of forest succession and its components.*

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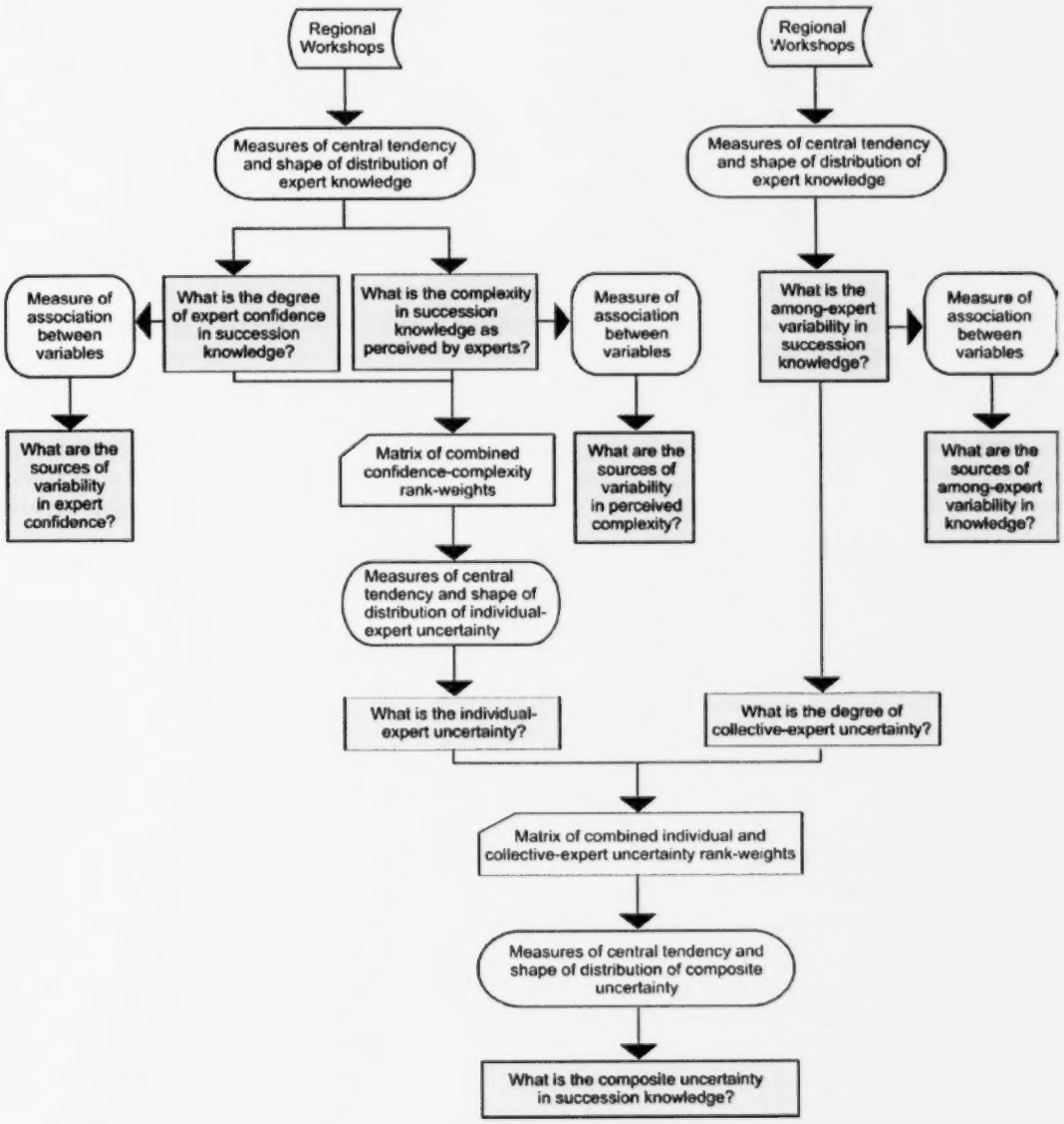
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Figure 4. *An overview of the analytical approaches used in assessing uncertainty of expert knowledge of forest succession and its components.*

We analyzed the distribution of composite uncertainty and of its components (individual and collective uncertainty) and sub-components (knowledge confidence and complexity) to assess relative levels of uncertainty. We used Theil's coefficient (Theil 1972 in SAS 1999) to analyze the association of knowledge confidence and complexity, and of collective uncertainty with ecological characteristics of transition rules, i.e., forest cover type, dominant leaf type (i.e., broadleaf, mixed, coniferous), and site conditions. Site conditions are described by their soil moisture regime (ranked from xeric to saturated) and nutrient regime (ranked from poor to rich, plus organic).

A more detailed description of the methodology of expert knowledge uncertainty assessment is provided by Drescher et al. (2006).

Results and discussion

Extent of expert knowledge of boreal forest succession

The exact extent of the overall expert knowledge body of boreal forest succession is unknown. Although the number of members in the Ontario Professional Foresters Association (>1,000 as of March 1998) suggests that the group of experienced practitioners is large, no concerted efforts have been made to formally explore and preserve the extent of expert knowledge of forest succession. We have to assume that with the recent retirement of many experienced individuals much knowledge may have been lost, and that the experiences of younger practitioners in second-growth forests may differ substantially from what their predecessors experienced in terms of natural dynamics.

Geographical limits of expert knowledge

The two published expert opinion reports (Ride et al. 2004, Vasiliauskas et al. 2004) suggest that expert knowledge of boreal forest succession in Ontario covers the entire AOU, which ends in the north roughly between 50° and 51° latitude. The large area of boreal forest north of the AOU has not been the subject of much study and as a result little information is available for experts to draw upon.

Types of forest transition

Expert knowledge about natural succession of forest cover types is provided for both regions, but that for post-fire establishment is provided only for northwest boreal Ontario (Ride et al. 2004).

Biological resolution

The two expert opinion reports (Ride et al. 2004, Vasiliauskas et al. 2004) express forest succession as changes in discrete forest cover types at the stand level. Average stand-level species composition of forest cover types is indicated but species-level changes in forest cover are only briefly mentioned in Vasiliauskas et al. (2004). A higher, network-level understanding of forest succession dynamics seems to be suggested by the simultaneous presentation of successional connections among all forest cover types in Ride et al. (2004), but this is not explicitly discussed.

Site conditions

No expert knowledge is provided about the effects of site conditions such as soil moisture and nutrient regimes on forest succession, though some minor remarks are made about the effects of extreme site conditions such as shallow, dry soils, on natural succession (Vasiliauskas et al. 2004).

Spatial resolution and extent

Expert knowledge of boreal forest succession is provided by ecogeographical unit (Ride et al. 2004, Vasiliauskas et al. 2004), but is not spatially explicit below this level. Instead, landscape-level proportions of stands undergoing forest cover type transitions are quantified. Variation at the sub-landscape level is acknowledged but not described and effects of spatial factors on forest succession are not mentioned.

Temporal resolution and extent

Expert knowledge about forest aging during succession is provided only for northeastern boreal Ontario (Vasiliauskas et al. 2004). All information applies to mature and overmature stands for which the start age and end age of natural succession is provided. Knowledge about mature stands may be more comprehensive because such stands cover most of the land base and changes in species composition may be relatively slower than in young or decaying stands. Personal observations of mature stands by experts may be more abundant and these stands may attract most attention from forestry experts because of their relatively higher economic value to the forest industry.

Stochasticity of forest succession

Expert knowledge of forest succession is expressed deterministically, on a proportional landscape area basis, which does not acknowledge the possibility of stochastic deviation from these deterministic values. However, Ride et al. (2004) do assume a certain level of expert uncertainty. Based on this uncertainty, extremes of deterministic values are defined and used to explore ranges of "conceivable" forest landscapes. The stochasticity of post-fire establishment or natural succession at the stand-level in terms of direction and timing of transition is not discussed.

Uncertainty of expert knowledge of boreal forest succession

Relative levels of knowledge uncertainty

Expert knowledge confidence and complexity were mainly medium for both post-fire establishment and natural succession. In combination, knowledge confidence and complexity led to high individual expert uncertainty for both forest transition types (Figure 5). Collective knowledge uncertainty of experts, however, differed between post-fire establishment and natural succession: Collective uncertainty was mainly very low for post-fire establishment and high for natural succession. In combination, individual and collective uncertainty led to medium to high composite uncertainty for post-fire establishment, but high composite uncertainty for natural succession (Figure 5).

The combination of high individual uncertainty with low collective uncertainty for post-fire establishment may indicate that individual experts are uncertain about their knowledge, but that they support each other collectively. This could be the result of a weak knowledge base that is shared among the experts as "common knowledge."

The difference in collective uncertainty between post-fire establishment (medium-high) and natural succession (high) leads us to hypothesize that wildfire has similar effects throughout the boreal forest and is relatively independent of local context, leading to similar experiences among experts. However, once wildfire effects have diminished through time, importance of local context increases, leading to differences in experiences among experts and consequent disagreement about natural succession.

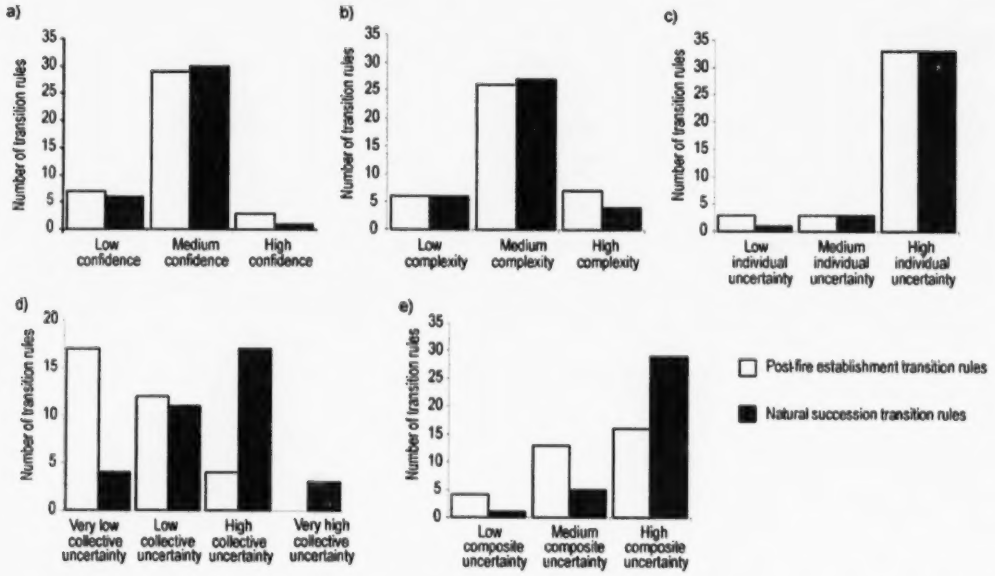


Figure 5. *Distribution of components of uncertainty for post-fire establishment and natural succession forest cover type transitions for Ontario forestry experts. The sub-figures show the distributions of reviewed transition rules for component levels. Components are (a) individual confidence, (b) individual perceived complexity, (c) individual uncertainty, (d) collective uncertainty, and (e) composite uncertainty. Concentration of transition rules in a component level indicates the general response of forestry experts.*

Sources of knowledge uncertainty

Expert knowledge confidence was associated with forest cover type for post-fire establishment (P = 0.023), but not for natural succession. Similarly, knowledge complexity for post-fire establishment was associated with forest cover type and leaf type (P = 0.014 and P= 0.025), and values were highest for mixed forest cover types. Depending on the expert group, knowledge complexity for natural succession was associated with forest cover type and leaf type (P = 0.001 and P = 0.008), and again values were highest for mixed leaf types. However, complexity for natural succession was also associated with soil moisture and nutrient regimes (P = 0.006 and P<0.001), and values were lowest for extreme site conditions such as xeric and poor or saturated organic. Collective uncertainty was associated with forest cover type and leaf type for post-fire establishment only (P = 0.004 and P= 0.001), and values were highest for mixed forest cover types.

The associations of high values of various components of uncertainty with mixed leaf types lead us to hypothesize that the higher diversity of species in mixed forests causes a higher diversity of natural succession trajectories leading to increasing uncertainty. At the same time, the association of low complexity with extreme site conditions leads us to hypothesize that extreme site conditions lead to more predictable natural succession trajectories resulting in decreased knowledge complexity.

General summary of findings

The results suggest that expert knowledge of boreal forest succession is available for the entire area of the undertaking. More knowledge seems to be available for natural succession in mature stands compared to post-fire establishment and dynamics in young and overmature stands. This contrasts with the increased knowledge uncertainty for natural succession compared to post-fire establishment (Table 2).

Table 2. *Significant associations of components of uncertainty in expert knowledge about forest succession with characteristics of transition rules (non-significant associations are denoted by a dash).*

Region	Succession type	Transition rule characteristic			
		Forest unit	Leaf type	Moisture regime	Nutrient regime
NE	Post-fire establishment	Confidence	-	-	-
	Natural succession	Confidence and complexity	Complexity	Complexity	Complexity
NW	Post-fire establishment	Among-expert variability	Among-expert variability	-	-
	Natural succession	-	-	-	-

Expert knowledge of forest succession captured in Ride et al. (2004) and Vasiliauskas et al. (2004) is expressed deterministically as landscape-level proportions of stands succeeding and does not normally indicate the stochasticity of succession, effects of spatial factors, or sub-landscape-level variation. This does not necessarily mean that expert knowledge ignores stochasticity, but may indicate lack of opportunities to infuse probabilities in applications. Much knowledge seems to be present on the stand-level, but scaling of stand-level dynamics to the landscape-level is limited to an arithmetic operation that uses landscape-level proportions of forest cover as a multiplication factor without considering stochastic or spatial factors. Effects of site conditions on forest succession appear less well known, though knowledge uncertainty was reduced for extreme site conditions. Variation in expert knowledge among forest cover types is not usually indicated, but uncertainty is higher for species-rich forests.

Based on these findings we conclude that expert knowledge is extensive but that its uncertainty is generally high. We hypothesize that expert uncertainty is a function of the strength of environmental control (e.g., by extreme site conditions) over forest cover type transitions and of species diversity. Uncertainty is highest for natural succession in species-rich forests under moderate site conditions (for details see Drescher et al. 2008).

Study limitations

Many practitioners with knowledge of boreal forest cover type transitions in certain geographic areas may not have been involved in the two expert opinion reports (Ride et al. 2004, Vasiliauskas et al. 2004) and their specific knowledge thus not captured in the study of expert knowledge uncertainty. The extent and resolution of their knowledge and their levels of uncertainty may differ for their local areas of expertise. However, our study scale was large and we worked with individuals who had extensive general knowledge over large geographic areas using a compilation of their knowledge. Our findings are therefore valid at these larger geographic scales.

Our approach of ranking uncertainty values and combining them in an additive model with specific parameters (weights) in the study of expert uncertainty is only one of a number of feasible approaches. However, preliminary analyses of results with other possible weightings showed that the general pattern of uncertainty remained stable. Therefore, we believe that even though other approaches may lead to other estimates of relative levels of uncertainty, the pattern of uncertainty and its association with ecological characteristics would remain similar and thus our findings remain generally valid.

Nature of published knowledge of boreal forest succession

Studies that have been published in the scientific literature are an important source of boreal forest succession knowledge. By applying a high-level framework, the information provided by numerous publications can be organized in a meaningful way to synthesize the embedded quantitative knowledge. This synthesized knowledge can then be explored to determine its extent and relative levels of uncertainty. Here we describe how we used a review of published studies of boreal forest succession to assess the extent of published knowledge, to determine areas of low and high knowledge uncertainty as well as to identify knowledge gaps whenever possible. We present the results of these assessments and discuss limitations of this component of the study.

Introduction

General characteristics of published knowledge of boreal forest succession

Knowledge of forest succession is provided by a vast body of published studies dating back to the 1930s (e.g., Clements 1936). Many studies of forest succession cover the boreal forests of North America and adjacent forest biomes (Yemshanov and Perera 2001). They include observational studies of post-disturbance re-initiation of stands and natural forest succession (e.g., Bergeron and Dubuc 1989), experimental studies into the effects of different disturbances on forest succession (e.g., Harvey and Brais 2002), and conceptual studies into basic principles of succession (e.g., Nobel and Slatyer 1980). These studies are published in a variety of formats such as research reports, theses, conference proceedings, and journal articles. Despite the wealth of information contained in these studies, few efforts have been made to integrate them into a coherent and synthetic body of knowledge, thus leaving isolated studies and the whole of the published knowledge largely fragmented. Moreover, the few efforts to integrate the body of knowledge are mostly published as general concepts (e.g., Viereck 1973, Pastor and Mladenoff 1992) and are not explored quantitatively. As a result, the extent and uncertainty of published knowledge about boreal forest succession is largely unknown and underutilized in subsequent studies of boreal forest succession.

Uncertainty of published knowledge

When considering the entire body of published knowledge, we can differentiate a number of factors related to uncertainty. First is the reliability of information provided by individual published studies. Studies vary in the rigour with which they are designed and implemented and studies of low rigour may present erroneous results with unclear partitioning of errors among measurement, sampling, and random error. Second is the variability of information among published studies. This variability can result from spatio-temporal variation in controlling factors or from their stochasticity. Incomplete documentation of the factors that may cause variation among studies impedes our ability to draw general conclusions about the processes controlling succession. Third is the amount of information provided by the whole of the published studies. The amount of information available increases with the number of studies aimed at the process in question and with the sample size of these studies. Generally, while the information provided by a small number of studies or samples could be greatly affected by sampling bias, the confidence and accuracy of the information is increased when the sample size is large. When reliability, variability, and amount of information is considered as an additive model, uncertainty of published knowledge decreases when the rigour (reliability) of studies is high, the variability among studies is low, and the number of studies and samples is high.

Methods

Extent and uncertainty of published knowledge

We explored the extent and uncertainty of the body of published knowledge of boreal forest succession in North America. We started with a review of the scientific literature and gathered all relevant publications in a literature database. All publications related to boreal forest succession broadly, with some focussing on specific processes such as seedling establishment (e.g., Charron and Greene 2002) within the larger context of forest succession, while others focus on forest succession itself (e.g., Bergeron and Dubuc 1989), or on modelling succession (Acevedo et al. 1996). The scale of studied processes varies from the individual stand to the landscape level.

All publications were rated based on (i) applicability and (ii) usefulness. Applicability was judged by the criteria of forest biome, geographic area, group of organisms, and process type (especially disturbance type). Applicable publications were only those focussing on (near) boreal forests, reporting on canopy tree species, and studying post-fire establishment or natural succession. Studies that reported relevant information from control plots were also included. Usefulness was judged by the criteria of originality of data, format of presentation, and quality of data. Useful publications were those reporting original data, reporting data for individual forest stands or small groups of stands, and indicating species composition and stand age or development stage. Only publications that were considered both applicable and useful were selected for further processing.

From the selected publications, we extracted data from figures, tables, and text including measurements such as basal area, surface cover, or number of individuals. We used these data to translate stand-level species composition into forest cover type using the same classification system as used in OMNR's northwest and northeast regions (Table 1). We extracted information about site conditions (soil moisture and soil nutrient regimes) using data such as surficial deposit type and slope position. We grouped all forest stand data records by forest cover types and used it to derive direction and timing (age at start and at maximum probability of succession) of forest cover type changes.

We used the extracted data to explore the extent of published knowledge of boreal forest succession in terms of its geographical and ecological coverage (i.e., forest cover types, leaf types, and site conditions).

We quantified uncertainty in published knowledge based on the relative amount of information provided for the process in question, assuming for the purposes of this study that reliability and variability are uniform over all studies.

Survey of on-going research

To assess the yet-to-be published forest succession knowledge, in 2005 we surveyed researchers in academia and government about ongoing forest succession studies in Ontario, Quebec, Manitoba, Minnesota, and Michigan. Information collected included geographies, spatial and ecological scales, timeframes, goals, treatments, experimental designs, hypotheses, and expected products.

Results and discussion

Extent and uncertainty of published knowledge

The literature database on boreal forest succession contained 828 scientific publications covering the period from 1900-2005. Based on our criteria for applicability and usefulness, we selected 63 publications (Appendix 1) and extracted 1,060 data records.

Geographic distribution

The selected publications cover the whole of the North American boreal forest biome. They cover the sub-divisions of this biome, described by Yemshanov and Perera (2001): southern boreal forest, the boreal mixedwood, and the northern boreal forest. Most publications (about three quarters) are about studies in boreal mixedwoods indicating relatively lower uncertainty for this sub-biome. Only one quarter of the publications reported on studies in southern and northern boreal forests indicating relatively higher uncertainty (Figure 6a). The majority of publications reported on studies from Quebec, followed by Ontario, and the Prairie Provinces. Almost three quarters of all studies were located in eastern North America indicating lower uncertainty for eastern boreal forests compared to western boreal forests (Figure 6b).

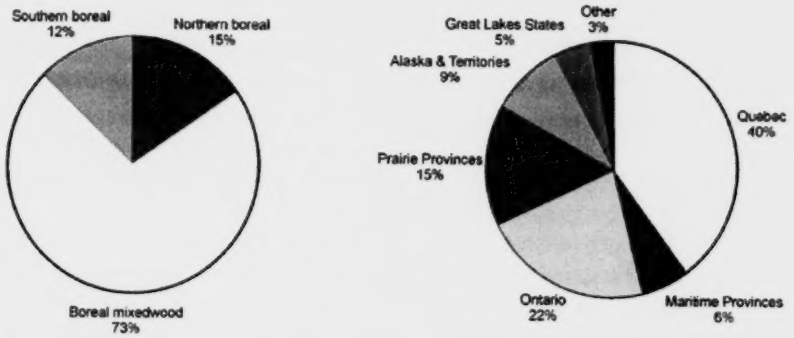


Figure 6. *Relative abundance of published reports (n=63) used to extract data about boreal forest succession by (a) forest biome and (b) geography.*

Distribution by type of forest transition

The number of data records providing information about the direction of natural succession was 323 (30%) and 291 (27%) for northwestern and northeastern forest cover type classifications, respectively. The number of data records that could be used for exploring timing of succession was 1,051 and 1,060 for northwestern and northeastern boreal Ontario, respectively. The number of data records that supplied information about direction of post-fire establishment transitions was much smaller than for the direction of natural succession: for each region, only 139 records (13%) from 9 publications (14%) supplied information about post-fire succession, indicating higher knowledge uncertainty for post-fire establishment relative to natural succession. Differences in number of records between regions result from incomplete information about species composition of stands that in some cases precluded unambiguous forest cover type classification.

Distribution by forest cover type

Data availability varied among forest cover types. For direction of natural succession, data were available for most forest cover types, but few data were available for red and white pine mixed, lowland conifer, and balsam fir, indicating highest uncertainty for these forest cover types. Most data available were for pioneer forests such as jack pine, hardwood, and trembling aspen indicating lowest uncertainty for these forest cover types (Table 3). Studies in these forest cover types also indicated very high records/studies-ratios indicating increased sampling intensity. For some forest cover types, such as the spruce bog type, no data were available, but these forest cover types were identified as completely self-replacing and no data about direction of succession was expected.

Table 3. *Number of data records and studies per forest cover type used in extracting data about* direction of natural succession *transitions. Note that a study may contain data for various forest cover types and may be enumerated more than once.*

Northwest Ontario				Northeast Ontario			
Standard forest unit	**Number of records**	**Number of studies**	**Records: studies ratio**	**Forest cover type**	**Number of records**	**Number of studies**	**Records: studies ratio**
PrDom	9	1	9.0	PR	9	1	9.0
PwDom	4	2	2.0	PW	4	2	2.0
PrwMx	1	1	1.0	PRW	1	1	1.0
OthHd	–[1)]	–[1)]	–[1)]	LH	–[1)]	–[1)]	–[1)]
HrDom	94	10	9.4	TH	–[1)]	–[1)]	–[1)]
SbLow	–[1)]	–[1)]	–[1)]	SB	16	2	8.0
PjDom	102	5	20.4	PJ1	85	5	17.0
OcLow	2	2	1.0	LC	2	2	1.0
PjMx	7	3	2.3	PJ2	7	3	2.3
SbDom	18	3	6.0	SP	11	4	2.8
BfDom	2	1	2.0	SF	4	2	2.0
PoDom	23	8	2.9	PO	103	12	8.6
BwDom	11	2	5.5	BW	21	7	3.0
SbMx	16	5	3.2	MW1	6	3	2.0
ConMx	26	8	3.3	MW2	22	9	2.4
HrdMw	8	2	4.0	SBOG	–[1)]	–[1)]	–[1)]

[1)] No Data.

For timing of natural succession, data was available for all forest cover types. Few data were available for lowland conifer forests, indicating highest uncertainty for this forest cover type. Most data available were for black spruce, jack pine, and trembling aspen forests, indicating relatively lower uncertainty for these forest cover types (Table 4). Again, the high records to studies-ratio indicated that sampling intensity for these forest cover types was highest.

For direction of post-fire establishment, knowledge gaps were identified for many forest cover types based on the absence of data. Absence of data was not related to successional status of forest cover types or abundance in the boreal forest biome. Most data available were for the black spruce and jack pine forests, indicating relatively lower uncertainty for these forest cover types (Table 5). The results again indicate higher uncertainty for post-fire establishment relative to natural succession.

Table 4. *Number of data records and studies per forest cover type used in extracting data about* timing of natural succession *transitions. Note that a study may contain data for various forest cover types and may be enumerated more than once.*

Northwest Ontario				Northeast Ontario			
Standard forest unit	**Number of records**	**Number of studies**	**Records: studies ratio**	**Forest cover type**	**Number of records**	**Number of studies**	**Records: studies ratio**
PrDom	16	5	3.2	PR	16	5	3.2
PwDom	28	5	5.6	PW	31	5	6.2
PrwMx	17	5	3.4	PRW	14	5	2.8
OthHd	–[1)]	–[1)]	–[1)]	LH	–[1)]	–[1)]	–[1)]
HrDom	60	16	3.8	TH	–[1)]	–[1)]	–[1)]
SbLow	–[1)]	–[1)]	–[1)]	SB	173	21	8.2
PjDom	172	20	8.6	PJ1	172	26	6.6
OcLow	10	4	2.5	LC	5	4	1.3
PjMx	41	15	2.7	PJ2	35	12	2.9
SbDom	207	23	9.0	SP	77	24	3.2
BfDom	62	15	4.1	SF	142	27	5.3
PoDom	130	20	6.5	PO	178	25	7.1
BwDom	35	9	3.9	BW	68	17	4.0
SbMx	66	22	3.0	MW1	14	7	2.0
ConMx	121	31	3.9	MW2	112	23	4.9
HrdMw	58	17	3.4	SBOG	–[1)]	–[1)]	–[1)]

[1)] No Data.

Table 5. *Number of data records and studies per forest cover type used in extracting data about direction of post-fire establishment transitions. Note that a study may contain data for various forest cover types and may be enumerated more than once.*

Northwest Ontario				Northeast Ontario			
Forest cover type	**Number of records**	**Number of studies**	**Records: studies ratio**	**Forest cover type**	**Number of records**	**Number of studies**	**Records: studies ratio**
PrDom	–[1)]	–[1)]	–[1)]	PR	–[1)]	–[1)]	–[1)]
PwDom	–[1)]	–[1)]	–[1)]	PW	–[1)]	–[1)]	–[1)]
PrwMx	–[1)]	–[1)]	–[1)]	PRW	–[1)]	–[1)]	–[1)]
OthHd	–[1)]	–[1)]	–[1)]	LH	–[1)]	–[1)]	–[1)]
HrDom	–[1)]	–[1)]	–[1)]	TH	–[1)]	–[1)]	–[1)]
SbLow	–[1)]	–[1)]	–[1)]	SB	53	5	10.6
PjDom	21	2	10.5	PJ1	21	2	10.5
OcLow	5	3	1.7	LC	5	3	1.7
PjMx	15	2	7.5	PJ2	15	2	7.5
SbDom	57	5	11.4	SP	18	6	3.0
BfDom	–[1)]	–[1)]	–[1)]	SF	1	1	1.0
PoDom	19	4	4.8	PO	19	4	4.8
BwDom	–[1)]	–[1)]	–[1)]	BW	–[1)]	–[1)]	–[1)]
SbMx	10	3	3.3	MW1	2	1	2.0
ConMx	9	3	3.0	MW2	5	1	5.0
HrdMw	3	1	3.0	SBOG	–[1)]	–[1)]	–[1)]

[1)] No Data.

Distribution by leaf type

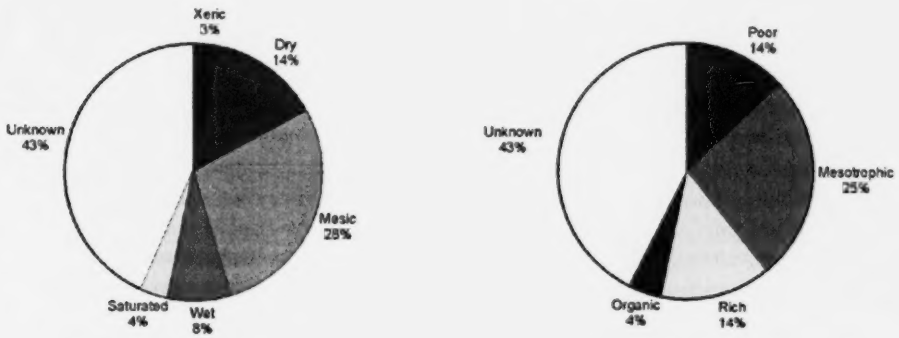
Data availability varied among leaf types. Generally, fewest data records were available for mixed forest cover types indicating higher knowledge uncertainty for this leaf type. As well, the low records/studies-ratio indicated lower sampling intensity. Most data available were for broadleaf and coniferous forests, indicating relatively lower uncertainty. However, for direction of natural succession, data availability was highest for broadleaf forests, whereas for direction of post-fire establishment succession, data availability was highest for coniferous forests (Table 6). This difference in data availability between broadleaf and conifer forests may reflect variation in the incidence of wildfires for these leaf types and indicates higher uncertainty for knowledge about post-fire establishment after the burning of broadleaf forests.

Table 6. *Number of data records and studies per forest cover type used in extracting data about direction and timing of natural succession as well as about direction of post-fire establishment transitions. Data were averaged over forest cover types after ordering by leaf type.*

Type of transition information	Leaf type	Northwest Ontario			Northeast Ontario		
		Number of records	**Number of studies**	**Records: studies ratio**	**Number of records**	**Number of studies**	**Records: studies ratio**
Direction of natural succession	Broadleaf	42.7	6.7	6.4	31.0	4.8	6.5
	Mixed	6.8	2.3	2.9	14.0	6.0	2.3
	Conifer	22.0	2.7	8.1	13.9	2.2	6.3
Timing of natural succession	Broadleaf	75.0	15.0	5.0	65.8	12.3	5.4
	Mixed	50.5	13.2	3.8	63.0	15.0	4.2
	Conifer	74.9	13.0	5.8	67.7	13.1	5.2
Direction of post-fire establishment	Broadleaf	6.3	1.3	4.8	4.8	1.0	4.8
	Mixed	2.0	0.7	3.0	3.5	1.0	3.5
	Conifer	15.4	2.1	7.2	11.3	1.9	5.9

Distribution by site conditions

Site conditions (soil moisture and nutrient regime) could be determined for less than two thirds of the stands (57%) reported in the published literature, indicating relatively little scientific interest into the effects of site conditions on forest succession. Most of these stands were located in areas with moderate site conditions: More than one quarter were on sites with a mesic moisture regime, followed by dry and wet sites, indicating relatively lower uncertainty for stands on mesic sites. One quarter of stands were located in areas with mesotrophic nutrient regime, followed by poor and rich sites, indicating relatively lower uncertainty for stands on mesotrophic sites (Figure 7).



(a) soil moisture regime

(b) soil nutrient regime

Figure 7. *Relative abundance of published reports (n=63) used to extract data about boreal forest succession by site condition.*

Extent of on-going research

Survey responses (n=25) indicated that more than half (56%) of all current research projects are focused on small-scale questions and specific forest cover types. Only 16% of responses indicated that research was focused on processes at the landscape-level or larger, while just 20% of responses indicated that research was underway that crossed organizational scales, usually from the species or community to the landscape-level. About one third (32-36%) of all ongoing studies included forests that have been disturbed through insect defoliation.

Most researchers defined medium forest age as >60 years, while they defined old as >150 years. Following the abovementioned definition of natural succession, forests of medium and old age may be expected to undergo natural succession, while forests of <10 years may still be in the post-fire establishment phase. The survey results indicated that more than 50% of all research activities also include studies of young post-fire forests stands. It is, however, unclear whether this can be interpreted as indicating research in post-fire establishment or rather in dynamics of young post-fire stands after the post-fire establishment phase has ended. As well, survey results indicated that more than 80% of research activities include studies of medium to old forest stands, indicating that research is directed mostly at natural succession and not post-fire establishment.

General summary of findings

Our results suggest that most knowledge is available for the relatively humid boreal mixedwoods of northeastern North America, indicating lower knowledge uncertainty for these forests compared to the boreal mixedwoods of northwestern and north-central North America and the northern boreal forests. Most knowledge seems to be available for natural succession of pioneer forest cover types such as jack pine and trembling aspen while little knowledge is available for lowland conifer and mixed red and white pine forests, indicating higher knowledge uncertainty for the latter forest cover types. Knowledge of post-fire establishment overall is weakly developed. Only for the black spruce forest cover type were data plentiful while for many forest cover types such as balsam fir forests no data were available, indicating knowledge gaps. The least knowledge is available for mixed forest cover types, indicating highest uncertainty for these forest types. Overall, little knowledge seems to be available about the effect of site conditions on forest succession, with especially high uncertainty about forest succession under moderate site conditions.

Study limitations

Limitations to our approach may arise from difficulty assessing all published studies of boreal forest succession. We identified and accessed studies mainly based on searches of electronic databases, thus our data may be biased towards recent journal publications. However, the general pattern of knowledge availability and uncertainty does not appear to differ significantly among older and more recent publications.

We based availability of knowledge about forest cover types on available groupings of forest stands that are based on tree species abundance and environmental factors. A level of uncertainty is associated with these groupings, however, our groupings are similar to those of forestry experts.

Uncertainty of knowledge is related to the reliability, variability, and amount of available information. However, in this study we based the quantification of uncertainty of published knowledge mainly on the amount of available information. Subsequent studies should include reliability and variability of information in the quantification of knowledge uncertainty.

Integrating expert and published knowledge of boreal forest succession

Formulating boreal forest succession knowledge from experts and from published studies as hypotheses in identical format allows these knowledge sources to be compared. Such a comparison reveals the level of congruence between the sources, and hypothesis pairs (expert vs. published knowledge) with low congruence may indicate an increased need for falsification of hypotheses. This is possible by comparing hypotheses to empirically observed forest succession to determine the level of support for each hypothesis. Emerging from this comparison is an integrated body of knowledge that is based on both knowledge sources with known congruence, strengths, and weaknesses. Here we explain how the hypotheses about natural succession through time were derived from the previously described knowledge sources as well as how they were compared and tested. We present the results of these steps and discuss some limitations of this component of the study.

Introduction

Expert knowledge about forest succession is often used in forest management planning (e.g., Marcot et al. 2001) and in deriving succession rules for applied forest succession models (e.g., Davis 1999). At the same time, a large body of published knowledge of forest succession has been accumulated during a century of research (e.g., Yemshanov and Perera 2001) and this wealth of information could be used to inform forest management. However, expert and published knowledge are not integrated and it is not known whether they are congruent and thus interchangeable. It is also unknown whether expert and published knowledge are accurate representations of forest succession at forest management relevant scales. Therefore, it remains unclear which knowledge source should best be used as a basis for forest resource management.

An integration of expert and published knowledge could be used to indicate areas of high vs. low information-richness and areas of concordance and discordance between knowledge sources. These signals could be used to direct research efforts towards knowledge gaps and to focus hypothesis testing efforts in areas of higher knowledge uncertainty. Expert and published knowledge can also serve as a basis for deriving alternative hypotheses of forest succession that can be tested against empirical observations to identify more accurate representations of forest succession that will better inform forest management.

Methods

Deriving hypotheses about natural succession from expert and published knowledge

Expert hypotheses

As the basis for expert hypotheses of boreal forest succession we used two reports (Ride et al. 2004, Vasiliauskas et al. 2004) that are considered compendia of regional expert knowledge. In these reports, the authors summarize expert opinion about forest succession between forest cover types in boreal Ontario based on landscape-level proportions of stands making these transitions. Ride et al. (2004) present expert opinion about natural succession for 21 ecogeographical regions in northwest and Vasiliauskas et al. (2004) present expert opinion about natural succession for two ecogeographical regions in northeast boreal Ontario.

We interpreted expert opinion about landscape-level proportions of stands making succession transitions directly as ecoregionally specific hypotheses about stand-level direction and probability of natural succession between forest cover types and of self-replacement. Expert opinion about forest ages at the start and end of succession was available for two ecogeographical regions in boreal northeast Ontario (Vasiliauskas et al. 2004) and was used as expert hypotheses about these forest ages.

Published knowledge hypotheses

We formulated hypotheses for published knowledge using data records contained in the entire literature database of boreal forest succession studies (see *Nature of published knowledge of boreal forest succession* section). Each data record consisted of forest cover type and age of a stand. When studies addressed stand succession, these records included additional information: the highest observed age for a stand (maximum age), forest cover type at maximum age, and the forest cover type to which the stand succeeded.

To derive hypotheses about the direction of succession, we grouped all data records by forest cover type and calculated the proportions of stands succeeding between cover types:

$$p_{ij} = \frac{n_j}{\sum_i n_i} \qquad (1)$$

where, n_j is the number of stands succeeding from forest cover type *i* to *j*, n_i is the total number of stands succeeding, and p_{ij} is the estimator of probability of succession from forest cover type *i* to *j*.

To derive hypotheses about timing of succession, we used the information about age class distributions of stands grouped by forest cover types:

$$c_{x_i} = \frac{n_{x_i}}{\sum_x n_{x_i}} \qquad (2)$$

where c_{x_i} is the relative frequency of stands of cover type *i* in age class *x*, and n_{x_i} is the number of cover type *i* of stands in age class *x*. We used this relationship to analyze the age class distribution of stands of each forest cover type *i* with simple life table methods (Caughley 2004) and derive the estimates of forest ages at start of succession and maximum probability of succession. The latter refers to the point in time when the largest proportion of stands is expected to succeed. (For a more detailed description of these methods, see Appendix 2).

To derive hypotheses about self-replacement, we imposed a double threshold rule (stand proportion and stand age). Specifically, if >10% of the stands of forest cover type *i* remained in *i* (i.e., had not switched to *j*) after reaching twice the estimated age at start of succession, then we assumed self-replacement of forest cover type *i*. This assumption[1] permitted us to assess whether self-replacement might occur or not, as a binary indicator.

We interpreted the proportions and binary indicators as hypotheses of stand-level direction and probability of succession between forest cover types and of self-replacement. These hypotheses were developed to be universally applicable throughout the boreal forests of North America and only differ between northwest and northeast Ontario because of the different forest cover type classification systems applied (Table 1).

Deriving forest succession models from hypotheses

Models are more specific formulations of hypotheses and are often used for their evaluation (Hilborn and Mangel 1997). We used the hypotheses of stand-level probabilities of natural succession and self-replacement to formulate models of forest landscape-level succession: Each hypothesis specifies the forest cover types to which it applies (forest cover types being identical for self-replacement). When all hypothesized probabilities are simultaneously connected among all forest cover types, a forest landscape-

[1]No information is available in literature on how to determine self-replacement. Even though our approach is an assumption, it assesses self replacement consistently for both expert and published knowledge sources.

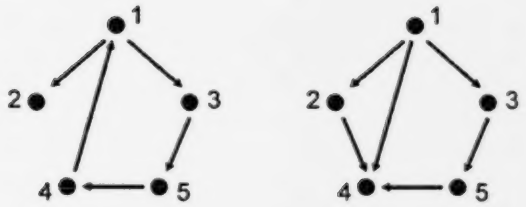


***Figure 8**. Illustration of hypothetical succession networks as graphs, where dots represent the forest cover types and lines the succession paths. They can be used to show differences and similarities among networks based on number of dots and lines and directions of lines.*

level network of succession emerges that can be graphically depicted (Figure 8). In this network, the *nodes* are the forest cover types and the *edges* are the succession relationships among the cover types. These networks are abstract models of forest succession, and in our case do not explicitly include information about the timing of succession (forest ages) or the effects of disturbances.

Using this approach, we derived expert succession networks specific to each ecogeographical region in boreal Ontario. In the same way, we derived succession networks for the published knowledge, which are applicable equally across boreal Ontario, but differ because of the different forest cover type classification systems used in northwest and northeast Ontario.

We formulated both expert and published knowledge succession networks as probabilistic and as binary networks. Probabilistic networks are based on the exact probabilities of succession among forest cover types, but do not include self-replacement. They provide information about which forest cover types succeed one another and the probability with which this occurs. Binary networks are based on a binary conversion of the probabilities of succession and self-replacement. They provide information about which forest cover types succeed one another and which ones are self-replacing, but only indicate whether such a transition/ self-replacement can occur (transition/self-replacement possible: yes/no) and not its probability.

Quantifying congruence between expert and published knowledge hypotheses

To evaluate congruence between expert and published knowledge hypotheses of forest succession, we quantified the levels of similarity between the succession network models and the level of similarity between the estimates of forest age at start of succession.

We quantified network similarity using two network-level indices that rely on basic principles of graph theory (Harary 1969). First, we developed the index of network similarity, S(L,E), and, second, we used Pearson's product-moment correlation, cor(L,E), for networks (for an explanation of these two indices, see Appendix 3). Both indices of network similarity are based on a comparison of the edges that run between the nodes in two graphs. For binary networks, the similarity of networks increases with the number of coinciding edges, i.e., edges that run between equivalent nodes and point in the same direction. For probabilistic networks, similarity of networks also increases with the number of coinciding edges, but in addition includes the probability value of the edge. The index of network similarity varies between 0.0 (no similarity) and 1.0 (identical), while Pearson's product-moment correlation varies between -1.0 (perfect negative correlation) and +1.0 (perfect positive correlation).

We calculated network similarity indices between expert and published knowledge succession networks for all 23 ecogeographical regions using both binary and probabilistic network forms. In this analysis, we assumed that increasing similarity indicated increasing congruence.

We quantified similarity between estimated forest ages at start of succession as the relative differences between age estimates, $T_i(L,E)$. For details of this calculation, see Appendix 3.

Empirical observations of boreal forest succession

We collected forest cover data from forest inventory plots and maps for seven ecogeographical regions in boreal Ontario (3S5, 4S2, 3W2, 3W3, 4W1, 3E Claybelt, and 3E Non-claybelt). Plot data were obtained from permanent inventory plots and plot-level aerial photography interpretation. Map data were obtained from standard forest resource inventory (FRI) maps and additional FRI-like maps. Plots as well as maps supplied stand-level information about canopy tree species abundance, canopy age, spatial location, and year of observation. The number of plots and map area varied among ecogeographical regions: Number of plots ranged from 28 to 298 and area ranged from 8,200 to 700,400 ha.

With the aid of a geographic information system, we selected all stands from plots and maps for which multi-year observations were available, resulting in more than 44,000 series of consecutive observations of forest cover types (with each series consisting of 2 or 3 observations). Stands originating from disturbances other than wildfire were excluded. The average minimum and maximum forest age over all series of observations was 9 and 248 years, respectively, while the overall average forest age of all observations was 67 years. Based on the observed species composition data, we determined the forest cover type (applying the classification systems used in northwest and northeast boreal Ontario, see Table 1) of all selected stands at the various time intervals. We interpreted the series of forest cover type observations as individual forest cover type time series for all individual forest stands. Then, based on all these individual series, we estimated probabilities of natural succession among forest cover types and of self-replacement for each ecogeographical region. Using the same approach as that used for deriving the succession network models for expert and published knowledge hypotheses, we connected the probabilities among all forest cover types and thus generated succession networks representing observed forest succession for each ecogeographical region. We expressed the observed forest succession network in its probabilistic and binary form.

Testing expert and published knowledge models of boreal forest succession

To evaluate whether expert and published knowledge succession network models are adequate representations of boreal forest succession, we compared them to the succession networks developed from the observed forest cover changes. We determined the level and significance of the similarity among the network models and used this information to assess the level of support for the expert and published knowledge succession network models.

Since the relationships among the nodes are not independent (edges that leave one node enter another node), classical hypothesis testing is not recommended for networks. Further, the underlying data structure generated by the relationships among the nodes is specific for these nodes and should therefore be preserved when generating reasonable null networks for hypothesis testing (Gotelli and Graves 1996). Thus, we required an alternate approach for testing among networks.

The quadratic assignment procedure (QAP, Hubert and Schultz 1976) is an algorithm used for the non-parametric testing of network-level statistics via Monte Carlo simulation of likelihood quantiles. Essentially a null model method (Gotelli and Graves 1996), QAP consists of the random permutation of rows and columns of a network-representing data matrix, thus creating null networks. By simultaneously permuting whole rows and columns, row and column marginals are preserved, diagonal cells remain on the diagonal, and the general underlying structure of the original network is explicitly maintained. Comparison of an observed statistic to the simulated distribution of the statistic for null networks allows an empirical assessment of the likelihood of the observed statistic. We modified the QAP (mQAP) by

relaxing assumptions about origins of the underlying network structure. The cells in each row of the data matrix represent the probabilities of succession from one forest cover type to other forest cover types and of self-replacement. This was the only underlying network structure relevant to us, and to maintain it, we only needed to preserve the row marginals. Accordingly, the mQAP consists of the random permutation of whole rows combined with random permutation of individual cells within rows. Otherwise, the mQAP approach mirrors that of QAP: We compared the similarity between a network hypothesis (expert or published knowledge) and an observed network to the distribution of similarities between null networks and the observed network. Accordingly, we tested the mQAP null-hypothesis that a network with equal or larger similarity to the observed network as the network hypothesis can simply be found as a random realization of permutations of matrix rows and cells.

We programmed the mQAP using the statistical programming language R, version 2.2.1 (R Development Core Team 2005) and constructed simulated distributions for null networks using 10,000 random permutations for each hypothesis test. We used the mQAP to separately test succession network hypotheses (expert and published knowledge) expressed as probabilistic and binary data matrices for all study regions.

Results and discussion

Expert and published knowledge models of boreal forest succession

Expert succession networks

Expert networks for ecogeographical regions in northwest Ontario (Table 7a, Figure 9a) suggest succession primarily leading from low shade-tolerance (low and high conifer content) to intermediate conifer content/ intermediate shade-tolerance and to high conifer content/high shade-tolerance. The black spruce and balsam fir forest cover types tend to form a distinct part of the networks towards which most succession transitions are directed.

Expert networks for ecogeographical regions in northeast Ontario (Table 7b, Figure 9c) suggest that pioneer cover types such as white birch or trembling aspen infrequently result from succession. They are, however, transient and most succession transitions are leading from them to other forest cover types. The majority of succession transitions lead from low shade-tolerance (low and high conifer content) to intermediate conifer content/intermediate shade-tolerance and to high conifer content/high shade-tolerance. The red pine and white pine forest cover types are only partially self-replacing and various succession transitions lead away from them. The black spruce bog, shade-tolerant broadleaf, and lowland broadleaf forest cover types are successional isolates and are not connected to other forest cover types.

Table 7. *Probabilities of forest cover transitions for succession networks based on expert and published knowledge for Ontario. Networks based on published knowledge are universally applicable throughout their respective Ontario region. Expert knowledge networks are examples from ecogeographical units (a) 3W3 and (b) 3E Claybelt. Published knowledge parameters show succession direction from forest cover type i to j, with probability of change (p_{ij}), excluding self-replacement. Self-replacement (p_{ii}) is indicated separately as a binary indicator (yes/no). Expert knowledge parameters show succession direction and probability, including self-replacement. For explanations of forest cover types see Table 1.*

(a) Northwest Ontario

Expert knowledge			Published knowledge		
Change between forest cover types		Self-replacement (p_{ii})	Change between forest cover types		Self-replacement (p_{ii})
From (i)	To (j, p_{ij})		From (i)	To (j, p_{ij})	
BF	SB, 0.30-1.00; SBMX, 0.30-1.00	0.30-1.00	BF	CONMX, 0.30-1.00	No
BRD	BRDMX, 0.30-1.00	0.00	BRD	BF, 0.10-0.30; SB, 0.30-1.00; CONMX, 0.10-0.30	No
BRDMX	CONMX, 0.30-1.00	0.10-0.29	BRDMX	CONMX, 0.30-1.00	No
			BRDOTH	–[1)]	Yes
BW	BRDMX, 0.30-1.00	0.10-0.29	BW	CONMX, 0.30-1.00	Yes
			CONLO	BF, 0.30-1.00	Yes
CONMX	BF, 0.30-1.00; SB, 0.10-0.30; SBMX, 0.30-1.00	0.00	CONMX	BF, 0.30-1.00; BRD, 0.10-0.30; BW, 0.10-0.30; SB, 0.10-0.30; SBMX, 0.10-0.30	Yes
PJ	PJMX 0.10-0.30; SB, 0.30-1.00	0.00	PJ	CONMX, 0.30-1.00; PJMX, 0.10-0.30; SB, 0.30-1.00	No
PJMX	SB, 0.30-1.00	0.00	PJMX	PJ, 0.10-0.30; SB, 0.30-1.00	Yes
PO	BRDMX, 0.30-1.00	0.00	PO	BRD, 0.30-1.00; CONMX, 0.10-0.30; SBMX, 0.10-0.30	No
			PR	BF, 0.10-0.30; CONMX, 0.30-1.00	Yes
			PRW	BRDOTH, 0.30-1.00	Yes
			PW	BF, 0.10-0.30; BW, 0.10-0.30; CONMX, 0.30-1.00	Yes
SB	BF, 0.30-1.00	0.30-1.00	SB	BF, 0.30-1.00; CONLO, 0.10-0.30; CONMX, 0.10-0.30; PJ, 0.10-0.30	No
			SBLO	–[1)]	Yes
SBMX	BF, 0.30-1.00	0.30-1.00	SBMX	BF, 0.10-0.30; CONMX, 0.30-1.00; SB, 0.10-0.30	Yes

[1)] Forest cover type *i* is completely self-replacing and does not change to any other forest cover type *j*.

(b) Northeast Ontario

Expert knowledge			Published knowledge		
Change between forest cover types		Self-	Change between forest cover types		Self-
From (i)	To (j, p_{ij})	replacement (p_{ii})	From (i)	To (j, p_{ij})	replacement (p_{ii})
BRDLO	--[1)]	1.00	BRDLO	--[1)]	Yes
BRDTO	--[1)]	1.00	BRDTO	--[1)]	Yes
BW	MWBRD, 0.35; MWCON, 0.30; PO, 0.05	0.30	BW	CONMX, 0.57; MWBRD, 0.38; PO, 0.05	No
CONLO	SB, 0.05	0.95	CONLO	CONMX, 1.00	Yes
CONMX	BW, 0.20; MWBRD, 0.40; MWCON, 0.10	0.30	CONMX	MWBRD, 0.25; SB, 0.75	Yes
MWBRD	BW, 0.05; CONMX, 0.20; SBPJ, 0.10	0.65	MWBRD	CONLO, 0.05; CONMX, 0.85; PO, 0.05; SB, 0.05	Yes
MWCON	BW, 0.05; SBPJ, 0.30	0.65	MWCON	BW, 0.66; PJSB, 0.17; PO, 0.17	No
PJ	MWCON, 0.20; PJSB, 0.80	0.00	PJ	CONMX, 0.08; PJSB, 0.13; SB, 0.42; SBPJ, 0.37	No
PJSB	MWCON, 0.20; SBPJ, 0.80	0.00	PJSB	PJ, 0.33; SB, 0.67	Yes
PO	BW, 0.10; MWBRD, 0.70; MWCON, 0.20	0.00	PO	CONMX, 0.25; MWBRD, 0.24; PJSB, 0.08; SB, 0.43	No
PR	MWCON, 0.10; PRW, 0.80	0.10	PR	CONMX, 1.00	Yes
PRW	CONMX, 0.20; MWBRD, 0.20	0.60	PRW	BRDTO, 1.00	Yes
PW	CONMX, 0.20; MWBRD, 0.20	0.60	PW	BW, 0.25; CONMX, 0.50; MWBRD, 0.25	Yes
SB	CONLO 0.05	0.95	SB	CONMX, 0.50; PJ, 0.19; CONLO, 0.31	No
SBPJ	CONMX, 0.40; MWBRD, 0.15; MWCON, 0.20	0.25	SBPJ	BW, 0.09; CONMX, 0.55; PO, 0.09; MWBRD, 0.09; SB, 0.18	No
SBLO	--[1)]	1.00	SBLO	--[1)]	Yes

[1)] Forest cover type *i* is completely self-replacing and does not succeed to any other forest cover type *j*.

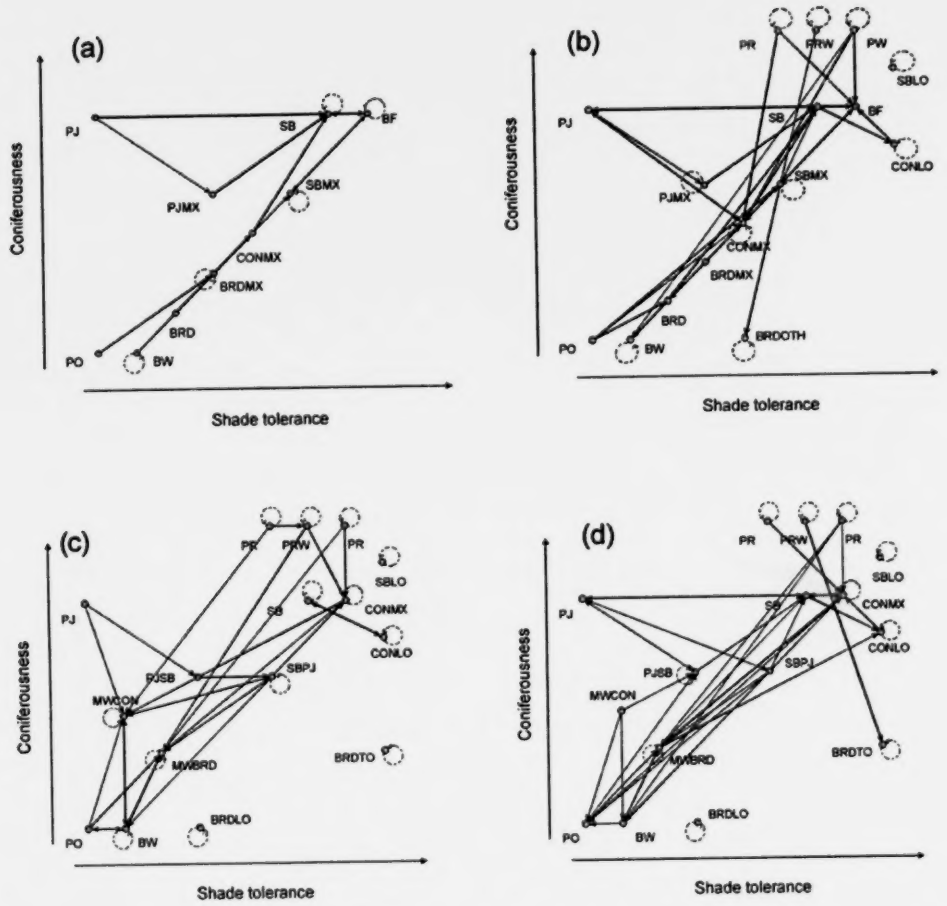


Figure 9. *Graphs of succession networks based on expert (a, c) and published (b, d) knowledge for northwest and northeast Ontario. The expert knowledge networks are examples from ecogeographical units 3W3 (a) and 3E Claybelt (c). Published knowledge networks are universally applicable throughout their respective regions (a, b: northwest Ontario, c, d: northeast Ontario). Dots represent forest cover types (for descriptions of cover types see Table 1) and are arranged by approximate conifer content and shade tolerance for illustrative purposes only. Succession is represented by arrows, with heads indicating the direction and weights indicating the approximate probability of succession. Self-replacement is indicated by dashed circular arrows as binary indicators (yes/no) only.*

The succession networks suggest the general course of succession through time. As an illustration, we follow the pathways of succession for four network steps, starting with the trembling aspen cover type as the original state (Figure 10a,c). The four network steps suggest succession from trembling aspen to a variety of mixed and conifer-dominated forest cover types. In some ecogeographical units, three succession steps may be needed before this variety of forest cover types is reached and a fourth step until succession converges towards a few forest cover types (northwest: mixed black spruce, black spruce, and balsam fir). In other ecogeographical units, a variety of forest cover types may be reached in just two succession steps with forest cover type changes converging in the third step (northeast: broadleaf mixedwood and coniferous mixedwood).

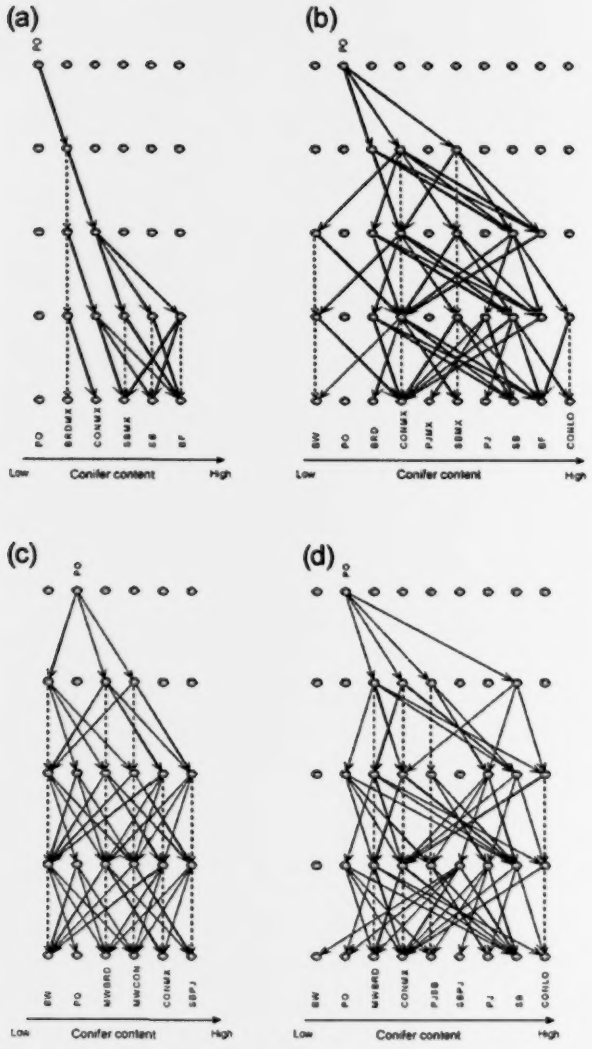


Figure 10. *Sequential steps of the example succession network presented in Figure 9 based on expert (a, c) and published knowledge (b, d) for northwest (a, b) and northeast (c, d) Ontario. Dots represent forest cover types (for descriptions of cover types see Table 1) and are arranged by approximate conifer content for illustrative purposes only. Rows of dots represent succession steps and not time intervals. Succession between forest cover types is indicated by arrows with weights indicating the approximate probability of succession. Self-replacement is indicated by dashed arrows as binary indicators (yes/no) only.*

Expert forest age estimates

Expert estimates of forest age at start of succession (Table 8) are lowest for pioneer forest cover types such as jack pine, white birch, and trembling aspen, and highest for red pine and white pine. Ages at the end of succession were estimated to be lowest for the jack pine forest cover type and highest for black spruce, lowland conifer, and red pine and white pine.

Table 8. Expert and published knowledge estimates of forest age at start of succession ($t_{L,start_i}$ for published knowledge and $t_{E,start_i}$ for expert knowledge), maximum probability of succession ($t_{L,\max_i}$ for published knowledge), and end of succession (t_{E,end_i} for expert knowledge) for Ontario. No expert information was available for northwest Ontario. For descriptions of forest cover types see Table 1.

Northwest Ontario			Northeast Ontario				
	Published knowledge			Published knowledge		Expert	
Forest cover type	$t_{L,start_i}$	$t_{L,\max_i}$	Forest cover type	$t_{L,start_i}$	$t_{L,\max_i}$	$t_{E,start_i}$	t_{E,end_i}
PR	150	170	SB	150	170	150	250
SB	150	170	PR	110	250	170	250
PW	110	130	PW	110	130	170	250
CONLO	110	130	CONLO	110	130	160	250
SBMX	110	130	CONMX	110	130	120	200
BF	110	130	MWCON	110	130	120	170
CONMX	110	130	PRW	90	110	170	250
PRW	90	110	SBPJ	90	110	120	200
BRDMX	90	110	MWBRD	90	150	120	170
BRD	70	90	PJ	70	90	100	150
PJ	70	90	PJSB	70	90	100	150
PJMX	70	90	PO	70	110	100	170
PO	70	130	BW	70	90	100	170
BW	70	130	BRDLO	–[1]	–[1]	–[1]	–[1]
BRDOTH	–[1]	–[1]	BRDTO	–[1]	–[1]	–[1]	–[1]
SBLO	–[1]	–[1]	SBLO	–[1]	–[1]	–[1]	–[1]

[1] Forest cover type *i* is completely self-replacing and does not succeed to any other forest cover type *j*.

Published knowledge succession networks

Published knowledge succession networks for northwest (Table 7a, Figure 9b) and northeast (Table 7b, Figure 9d) Ontario suggest succession from forest cover types with low shade-tolerance (low and high conifer content) to forest cover types with medium conifer content/shade-tolerance and high conifer content/ shade-tolerance. Though networks suggest that pioneer forest cover types, such as jack pine or trembling aspen, can infrequently result from succession, most transitions lead away from them. The red pine and white pine cover types are only partially self-replacing and tend to succeed to mixed conifer forests. Black spruce bogs are totally self-replacing and are not connected to other forest cover types. Some forest cover types show more successional connections than others, suggesting they have important positions in the succession networks (i.e., mixed conifer and balsam fir in the northwest and mixed conifer and broadleaf mixedwood in the northeast).

The succession networks suggest the general course of succession through time. As an illustration, we follow the pathways of succession for four network steps, starting with the trembling aspen cover type as the original state (Figure 10b,d). The initial network step suggests succession from trembling aspen to a variety of broadleaf, mixed, and coniferous forest cover types. This step leads to at least one third of the relevant cover types. The second step reaches at least two thirds of the forest cover types. With the third step, the diversity of forest cover types is further increased, but succession converges towards a few conifer-dominated forest cover types (i.e,, mixed conifer, black spruce, and balsam fir in the northwest and mixed conifer and black spruce in the northeast). The fourth step generally reinforces the succession pattern of the previous step.

Published knowledge forest age estimates

Published knowledge estimates of age at start of succession (Table 8) were lowest for pioneer forest cover types such as white birch, trembling aspen, and jack pine and highest for black spruce and red pine. The lowest ages for maximum probability of succession were estimated for the jack pine forest cover types and the highest ages for black spruce and red pine.

Congruence between expert and published models of boreal forest succession

We quantified expert and published knowledge congruence about direction of succession and present results at both the forest cover type and complete succession network level.

Results of expert and published knowledge congruence at the forest cover type level, S(L,E), were calculated for binary networks and averaged over ecogeographical units in northwest and northeast Ontario (Table 9). For the northwestern ecogeographical units, congruence was highest for the jack pine forest cover type and lowest for the broadleaf pioneer forest cover types as well as mixed jack pine and balsam fir. Congruence for most mixed and conifer-dominated forest cover types was intermediate. Using ecogeographical unit 3W3 as an example, we found that, in 50% of cases, expert and published knowledge agreed about the binary indicator of self-replacement (p_{ii}, yes/no) (Figure 9a,b), which is not significantly higher than would be expected by chance ($\chi = 0.00$, df = 1, P = 1.000). For the northeastern ecogeographical units, congruence was complete for the fully self-replacing, shade-tolerant lowland forest cover types (shade-tolerant broadleaf, lowland broadleaf, and black spruce bog). Apart from the fully self-replacing forest cover types, congruence was highest for white pine and lowest for mixed jack pine-black spruce. For a large and diverse group of broadleaf, mixed, and conifer forest cover types, congruence was intermediate. Using the 3E Claybelt ecogeographical unit as an example, we found that, in 69% of cases, expert and published knowledge agreed about the binary indicator of self-replacement (Figure 9c,d), which is not significantly higher than would be expected by chance ($\chi = 2.25$, df = 1, P = 0.134).

Table 9. *Similarity between expert and published knowledge succession networks, $S_i(L,E)$, in Ontario at forest cover type level i. $T_i(L,E)$ is similarity between expert and published knowledge estimates of forest ages at start of succession, at forest cover type level i. Mean values are averaged over ecogeographical regions. Expert estimates of forest ages could not be determined for northwest Ontario. For descriptions of forest cover types see Table 1.*

Northwest Ontario			Northeast Ontario				
Forest cover type	$S_i(L,E)$		Forest cover type	$S_i(L,E)$		$T_i(L,E)$	
	Mean	St. dev.		Mean	St. dev.	Mean	St. dev.
PJ	0.72	(0.11)	BRDTO	1.00		--[2]	--
BRDMX	0.55	(0.13)	SBLO	1.00		--[2]	--
SBMX	0.54	(0.17)	BRDLO	1.00		--[2]	--
CONMX	0.53	(0.16)	PW	0.86		0.57	
CONLO	0.50	(0.00)	CONMX	0.57		0.91	
SB	0.26	(0.19)	BW	0.57		0.65	
PJMX	0.09	(0.18)	CONLO	0.50		0.63	
BW	0.02	(0.11)	SBPJ	0.44	(0.00)	0.71	
BF	0.02	(0.09)	MWBRD	0.44		0.71	
BRD	0.00	(0.00)	SB	0.40		1.00	(0.00)
PO	0.00	(0.00)	PR	0.40		0.57	
SBLO	--[1]	--	PRW	0.40		0.38	
PW	--[1]	--	MWCON	0.33		0.91	
PRW	--[1]	--	PJ	0.33		0.65	
PR	--[1]	--	PO	0.29		0.65	
BRDOTH	--[1]	--	PJSB	0.00		0.65	

[1] No expert knowledge available about direction of succession.
[2] No published knowledge or expert estimates about forest age at start of succession since both sources indicate complete self-replacement.

Results of expert and published knowledge congruence at the complete succession network level were calculated for binary and probabilistic networks and are presented for each ecogeographical unit in northwest and northeast Ontario (Table 10). Using the index of edge similarity, S(L,E) as an example, we found that overall congruence between expert and published knowledge networks was low to intermediate (binary models: S(L,E) = 0.23 - 0.48; probabilistic models: S(L,E) = 0.19 – 0.44) and varied spatially among ecogeographical regions (Figure 11). For binary networks, expert and published knowledge networks were most congruent for the southeast ecogeographical regions 3E Claybelt and 3E Non-claybelt and least congruent for northwest Ontario ecogeographical regions 3S1, 3S3, and 4S1. For probabilistic networks, congruence was highest for ecogeographical region 3W3, while congruence for 3E Claybelt and 3E Non-claybelt was intermediate. Congruence was lowest for 3S2 and several other ecogeographical regions in the northwest.

Table 10. *Similarity of expert and published knowledge succession networks for 23 ecogeographical regions in boreal Ontario. Similarity is determined by the index of network similarity S(L,E), and Pearson's product-moment correlation coefficient cor(L,E), for binary and probabilistic formulations of the succession networks.*

Ecogeographical region	S(L,E)		cor(L,E)	
	Binary	Probabilistic	Binary	Probabilistic
3E Claybelt	0.48	0.26	0.37	0.21
3E Non-claybelt	0.48	0.26	0.37	0.21
3W3	0.43	0.44	0.27	0.36
4S4	0.42	0.36	0.25	0.28
5S2	0.42	0.41	0.25	0.35
3W5	0.41	0.37	0.23	0.27
3W2	0.38	0.31	0.20	0.22
4S5	0.38	0.36	0.20	0.25
4W2	0.38	0.36	0.20	0.26
3W1	0.35	0.32	0.18	0.20
3W4	0.35	0.39	0.18	0.29
2W2	0.33	0.29	0.14	0.16
3S4	0.32	0.24	0.16	0.10
4S2	0.32	0.33	0.16	0.24
3S5	0.31	0.23	0.14	0.08
4S3	0.31	0.34	0.14	0.26
4S6	0.31	0.27	0.14	0.17
2W3	0.30	0.25	0.08	0.10
3S2	0.30	0.19	0.10	0.03
4W1	0.26	0.22	0.04	0.09
3S1	0.23	0.23	0.04	0.09
3S3	0.23	0.20	0.04	0.06
4S1	0.23	0.23	0.04	0.13

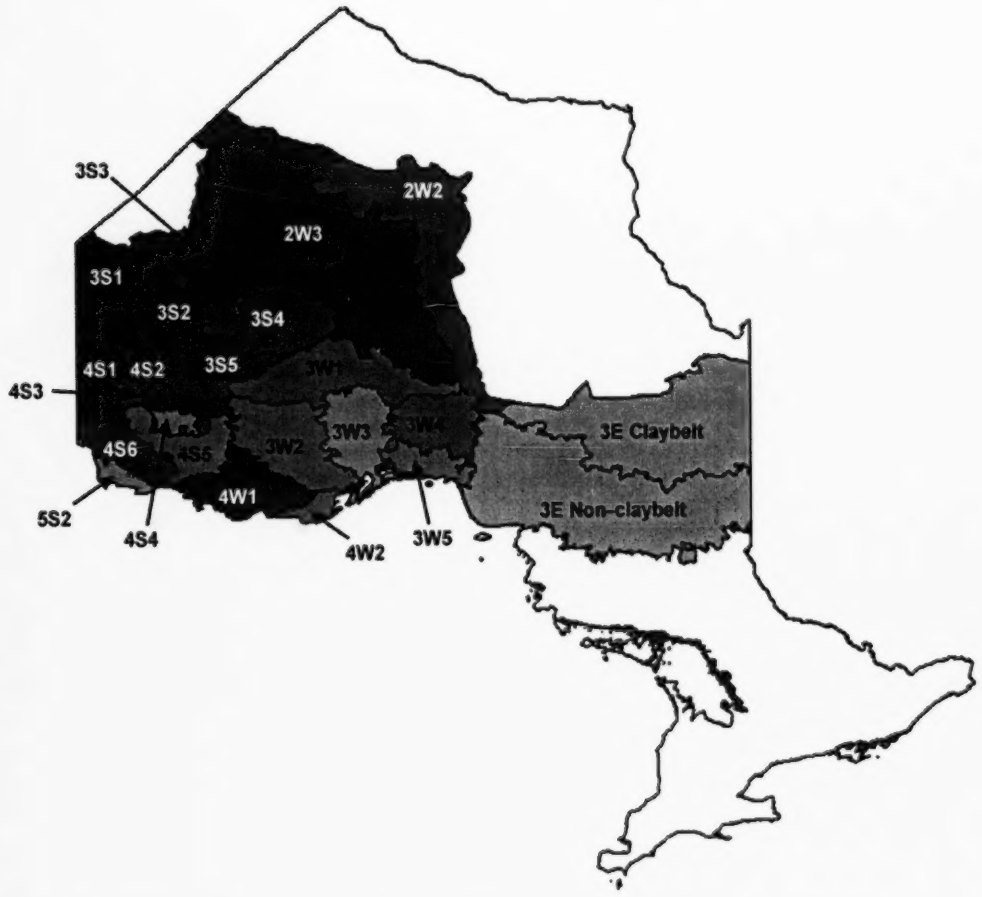


Figure 11. *Similarity as measured by index of edge similarity (S_{LE}) between binary expert and published knowledge succession networks for ecogeographical regions in boreal Ontario. Lighter shades indicate higher similarities.*

The variation in congruence between expert and published knowledge networks can be explained in part by the complexity of expert networks (i.e., number of edges in networks: $R^2 = 0.47$, $F_{1,19} = 17.11$, $P < 0.001$). The remaining variation, however, has to be attributed to the specific structure of the various networks. Kendal's rank correlation test indicated that the same pattern of congruence emerged regardless which similarity index was used (S(L,E) or cor(L,E) (binary networks: $\tau = 0.91$, $P < 0.001$; probabilistic networks: $\tau = 0.86$, $P < 0.001$).

We quantified expert and published knowledge congruence about timing of succession and present results at forest cover type level (Table 9). Congruence of expert and published knowledge estimates of forest age at start of succession, $T_i(L,E)$, was highest for the black spruce forest cover type and lowest for mixed red and white pine. A general pattern in this variability did not emerge, but four of the five forest cover types with highest congruence correspond to those forest cover types towards which succession converges in both expert and published knowledge succession networks (see Figure 10). Expert and published knowledge estimates were positively correlated ($\tau = 0.69$, $P < 0.001$). However, published knowledge estimates were consistently lower with an average difference of about 35 years. Expert estimates of end age of succession and published knowledge estimates of age at maximum probability of succession (Table 8)

describe different phenomena and should not be directly compared. We found, however, that both age type estimates were positively correlated ($\tau = 0.44$, $P = 0.024$), as would be expected.

Testing expert and published knowledge models of boreal forest succession

We compared expert and published knowledge succession networks to observed succession networks in seven ecogeographical regions (Figure 12). Here, we explicitly discuss only the results obtained using the index of edge similarity, S(L,E). The results from using Pearson's product-moment correlation, cor(L,E), are very similar (binary networks: $\tau = 0.58$, $P = 0.003$; probabilistic networks: $\tau = 0.64$, $P = 0.001$) and are shown as additional support for the patterns revealed by the index of edge similarity. Overall, the results of the network testing revealed that none of the expert or published knowledge succession networks were very similar to the observed succession networks (S(L,E) = 0.23 – 0.61) (Table 11).

For binary succession networks, similarity between networks and observations ranged from 0.30 to 0.61 (Table 11). Overall, published knowledge networks were more similar to observed networks than expert networks: In five ecogeographical regions (3S5, 3W3, 4W1, 3E Claybelt, and 3E Non-claybelt) published knowledge networks were more similar to observations than were expert networks, in one (4S2) both expert and published knowledge networks were equally similar to the observations, and in another (3W2) the expert network was more similar to the observations. All succession networks from both sources were supported by test results with few exceptions. The succession networks not supported ($P < 0.05$) were those from published knowledge in ecogeographical region 3W2, from expert knowledge in 3W3, and from both the published knowledge and expert networks in 4W1 (Table 11).

For probabilistic succession networks, similarity between networks and observations ranged from 0.23 to 0.56 (Table 11). Again, published knowledge networks were more similar to observed than expert networks: In five ecogeographical regions (3S5, 4S2, 3W3, 4W1, and 3E Claybelt) the published knowledge networks were more similar to the observations than were the expert networks. However, in two ecogeographical regions (3W2 and 3E Non-claybelt) expert networks were more similar to the observations. All networks were supported by test results except for the expert network in ecogeographical region 4W1 ($P < 0.05$).

Similarity of expert or published knowledge networks to observed networks was usually lower for probabilistic networks than for binary networks. This indicates that knowledge about the general pathways of succession (succession possible: yes/no) is more accurate than knowledge about the probability of succession, as might be expected.

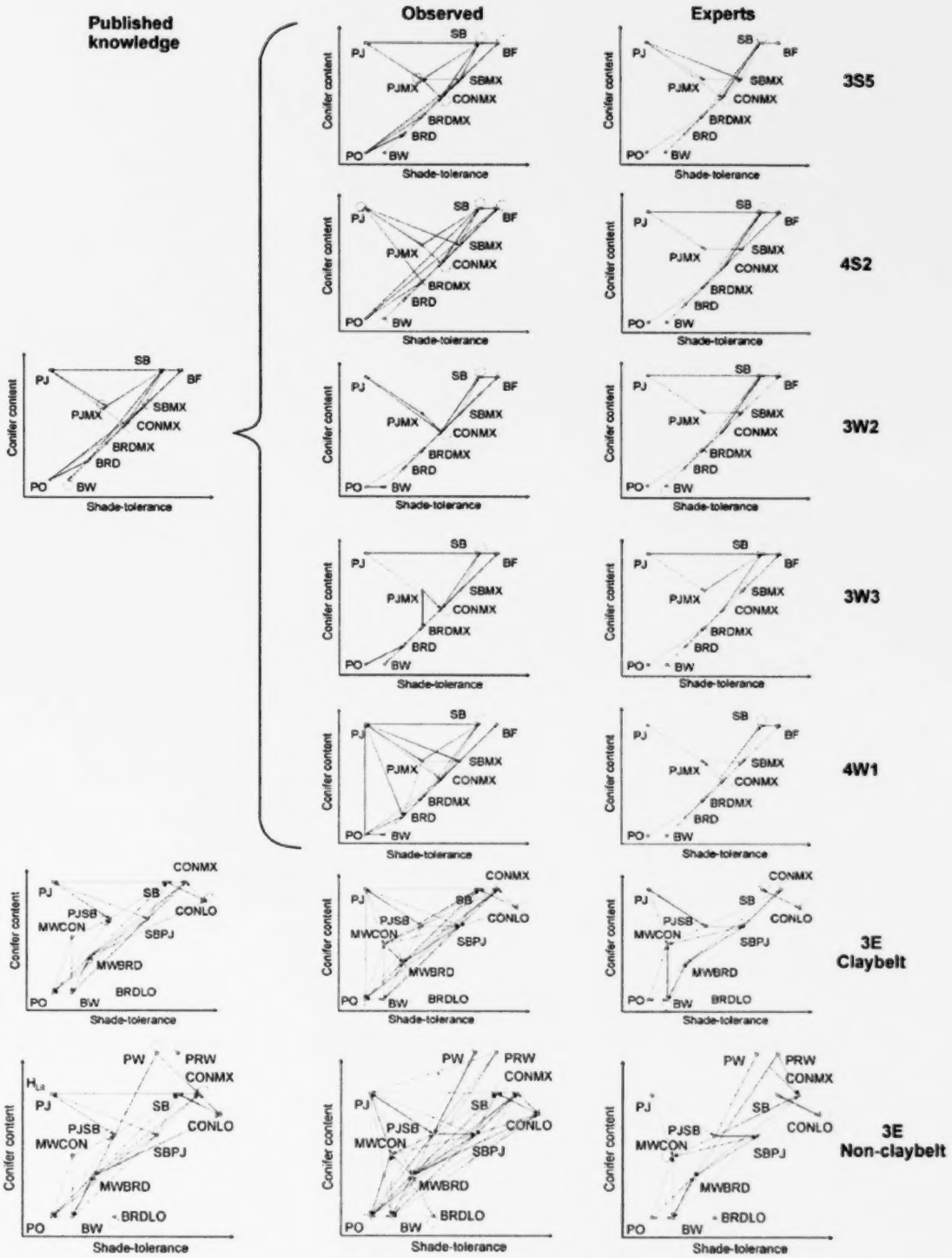


Figure 12. *Published knowledge (left) and expert (right) succession networks compared to the corresponding observed succession networks (centre) for seven ecogeographical regions in boreal Ontario. Dots and abbreviations indicate forest cover types (for descriptions see Table 1); lines indicate possible succession pathways among forest cover types and dotted circles possible self-replacement.*

Table 11. *Results of testing of expert and published knowledge succession networks for seven ecogeographical regions in boreal Ontario. Similarity between models and data was quantified with the index of edge similarity, S(L,E), and with Pearson's product-moment correlation for networks, cor(L,E), both for binary and probabilistic forms of the succession networks. The level of significance for similarity index and correlation coefficient values is indicated as *** P <0.001, ** P <0.01, * P <0.05, and ns P >0.05 (shaded).*

Study region	Hypothesis source	S(L,E)		cor(L,E)	
		Binary	Probabilistic	Binary	Probabilistic
3S5	H_{Lit}	0.58 ***	0.56 ***	0.41 ***	0.44 ***
	H_{Exp}	0.47 ***	0.35 **	0.37 ***	0.28 **
4S2	H_{Lit}	0.52 **	0.48 ***	0.30 **	0.41 ***
	H_{Exp}	0.52 ***	0.45 ***	0.41 ***	0.39 ***
3W2	H_{Lit}	0.36 ns	0.35 *	0.16 ns	0.23 *
	H_{Exp}	0.50 ***	0.44 ***	0.38 ***	0.35 **
3W3	H_{Lit}	0.49 **	0.51 ***	0.29 **	0.47 ***
	H_{Exp}	0.30 ns	0.33 *	0.10 ns	0.23 *
4W1	H_{Lit}	0.37 ns	0.35 *	0.11 ns	0.17 ns
	H_{Exp}	0.33 ns	0.23 ns	0.15 ns	0.08 ns
3E Claybelt	H_{Lit}	0.61 ***	0.48 ***	0.37 ***	0.41 ***
	H_{Exp}	0.52 *	0.40 ***	0.24 *	0.48 ***
3E Non-claybelt	H_{Lit}	0.56 ***	0.37 ***	0.40 ***	0.29 **
	H_{Exp}	0.49 ***	0.41 ***	0.32 ***	0.51 ***

General summary of findings

Congruence between expert and published knowledge networks was generally low though variable among ecogeographical regions. The lowest congruence was found for regions in the far northwest and the highest for those in southeast boreal Ontario, which can be explained by the complexity of the succession networks and the specific network structures. Similarity of expert or published knowledge succession networks to observations was low and varied among regions. Relative support for networks, quantified as mean similarity for binary and probabilistic model forms (moderate: $\overline{S} > 0.5$, low: $\overline{S} > 0.4$, absent: similarity not significant for either network form) showed that for all regions, except 3W2, support for published knowledge networks was as high as or higher than that for expert networks (Table 12).

Based on the results of congruence between expert and published knowledge networks, we conclude that uncertainty about boreal forest succession knowledge may be highest for ecogeographical regions in the far northwest of Ontario. From the network testing results, we conclude that the ecogeographically specific hypotheses of forest succession based on expert opinion did not always match observations well and did not fully capture the ecogeographical differences in succession. The universal hypotheses based on published knowledge often matched observations of succession better than expert hypotheses as well as capturing ecogeographic similarities in forest succession.

Table 12. *Relative level of support for expert and published knowledge networks based on their similarity to observed forest succession measured as index of edge similarity, S(L,E), averaged over binary and probabilistic forms of the succession networks. Relative level of support is moderate (++, $\overline{S} > 0.5$), low (+, $\overline{S} > 0.4$), or none (0; when similarity for either the binary or probabilistic form of the succession network was not significant).*

Knowledge source	Ecogeographical region						
	3S5	4S2	3W2	3W3	4W1	3E Claybelt	3E Non-claybelt
Published reports	++	+	0	+	0	++	+
Experts	+	+	+	0	0	+	+

Study limitations

The succession network testing approach indicates the overall similarity of the whole succession network to observed succession but, when networks are not similar, does not indicate the source of the dissimilarity. To accomplish this, information at the sub-network level could be acquired using local network statistics such as network degree analysis.

The lack of fit between the ecogeographically specific expert networks and the observations does not imply that succession among ecogeographical regions does not differ. It only means that the variation among the expert networks did not match the possible variation in observations among regions. The lack of fit could therefore be due to the absence of variation among regions or variation that is structured differently than that suggested by the expert networks.

Observed forest succession networks were based on forest cover type interpretations of data from historic and more recent forest inventory plots and maps. Changes in inventory protocols, photo-interpreters, and photo-interpretation standards over time may have affected tree species composition interpretations of aerial photography and plot measurements. Associated errors related to species composition and canopy age interpretations were not quantified for the selected forest stands and may differ among ecogeographical regions, forest cover types, and information sources (Thompson et al. 2007). To our knowledge the vast majority of our forest cover observations were not biased against succession-related stand mortality, but we cannot state this with absolute certainty for the entire data set. A level of uncertainty is therefore not only associated with expert opinion and published knowledge of forest succession, but also with observed forest cover type changes.

The fact that our approach is atemporal and does not include post-disturbance dynamics, increases its level of abstraction. However, it provides a framework for organizing corresponding hypotheses and observations, thus putting them on "equal footing" (cf. Failing et al. 2007) and forming an objective basis for their comparison. Since this abstract framework was applied equally to expert opinion, published information, and observed data, our findings are not artifacts of the method but reveal embedded, underlying differences among the expert/published knowledge networks and the observations.

Characteristics of the knowledge space

In this section, our goals are to describe the overall boreal forest succession knowledge space as relevant to Ontario and to recommend major areas where research is required to address the gaps. The views of the authors in this section reflect insight gained while conducting the studies and should not be deemed "conclusions." The objective here is to derive syntheses and abstract depictions of the overall knowledge space and extend recommendations for future research. Our assertions will be useful in formulating further research studies and specific testable hypotheses.

This knowledge space can be viewed using axes of relative uncertainty in expert and published knowledge. On these axes we placed dichotomous groups (e.g., natural succession and post-fire establishment) of characteristics relevant to boreal forest succession discussed in previous sections (Figure 13). Though both axes are categorically scaled to the same two classes (low and high), we do not imply that class width is the same between or within axes. Also, ranking into classes is independent for each dichotomous pair, i.e., the difference in uncertainty between the members in one pair does not need to be the same as in the other pairs.

We discuss the details of the knowledge space as grouped by these characteristics:

- phases of boreal forest succession (post-fire establishment vs. natural succession),
- boreal forest cover type of different species composition or leaf type (conifer and broadleaf stands vs. mixed stands),
- ranges of site conditions (moderate vs. extreme site conditions), and
- spatial and organizational level of forest cover (stand vs. landscape-level).

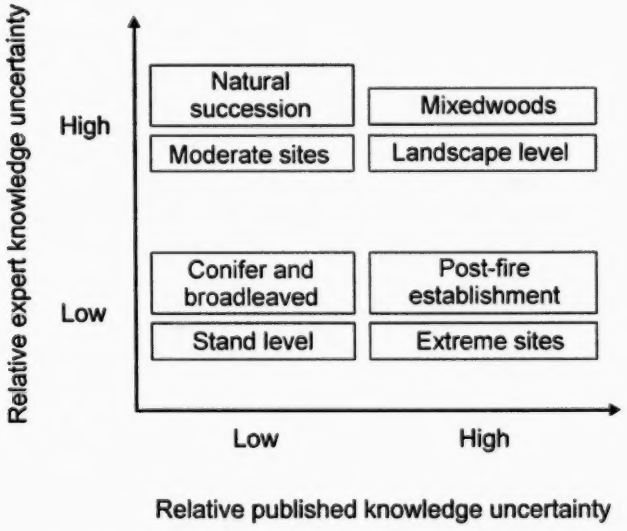


Figure 13. *An abstracted depiction of the space of boreal forest succession knowledge by using dimensions of relative uncertainty in expert knowledge and in published knowledge. Axes of relative uncertainty are categorically scaled into classes (class widths are not uniform and the rankings of dichotomous pairs are independent).*

Phases of boreal forest succession

Uncertainty in expert knowledge about post-fire establishment is relatively lower than that for natural succession, possibly as a result of a temporarily homogenizing effect of wildfire on early vegetation dynamics that may minimize neighbourhood effects and increase predictability. Moreover, Ride et al. (2004) present highly precise expert opinion on post-fire establishment trends on a continuous scale, which suggests a low degree of uncertainty and a large underlying information base. However, the extent and biases of this evidence base are not known. In contrast, uncertainty of published knowledge about post-fire establishment is generally high, with the exception of the pioneer forest cover types black spruce, jack pine, or trembling aspen. As may be expected, it is especially high for the non-pioneer cover types, for which very little information was found. Rigorous investigations of post-fire establishment at appropriate spatial scales are scarce even though some studies report the effects of micro-environment on seedling establishment (e.g., Lee 2004). A reason for the scarcity of studies of post-fire establishment might be that accurate and precise information about pre-fire conditions are seldom available.

Expert knowledge of natural succession is expressed only as generalized trends (e.g., Ride et al. 2004), and the uncertainty in this knowledge is relatively higher than for post-fire establishment. This is likely because the natural succession process is more complex: it unfolds over many years, possibly several centuries, and the homogenizing effects of wildfires weaken through time (Oliver and Larson 1990), releasing natural succession from the relatively strong control of wildfire conditions and exposing it to more complex neighbourhood effects (Galipeau et al. 1997) and other factors such as prevailing climate (Peters et al. 2006). However, published knowledge of natural succession is more abundant, and has a relatively lower uncertainty compared to that of post-fire establishment. Published knowledge about natural succession was only absent for few forest cover types, such as lowlands under extreme site conditions that are assumed to be fully self-replacing. Many reasons may contribute to the abundance of published knowledge on natural succession, for example, the ready availability of study sites (i.e., forest stands past the initialization phase); and economic and ecological interests in mature forest stands.

We recommend that research activities into post-fire establishment of boreal forests be undertaken to increase knowledge of the associated processes and to support a rigorous evaluation of the expert knowledge currently used for forest management purposes. This recommendation is in agreement with Lecomte and Bergeron (2005), who extended a hypothesis that differences in fire severity may have pronounced effects on dynamics in young post-fire forest stands that needs to be evaluated by further research. Furthermore, Johnstone and Chapin (2006a,b) found that wildfire intensity and frequency can have immediate and lasting effects on post-fire stand dynamics. These studies illustrate the need for more detailed research into how wildfires affect boreal forest succession. In the interim, expert opinion may be considered an important knowledge source in addressing information needs as well as in formulating research hypotheses. We consider that it is possible to treat both expert and published knowledge as hypotheses and formulate models of natural succession, which can be tested against empirical observations of forest cover changes to evaluate the level of local accuracy of the current knowledge.

Forest leaf types

Expert knowledge uncertainty was relatively lower for succession of coniferous forest cover types than for broadleaf forest cover types. This may be due to the relative simplicity of species compositions of the former: though coniferous forest cover types can be species-rich, most coniferous forests are dominated by one species, often jack pine, black spruce, or balsam fir, depending on the stage of succession (Ride et al. 2004, Vasiliauskas et al. 2004). Boreal broadleaf forest cover types are usually dominated by shade-intolerant white birch or trembling aspen, or are a mix of those species (Ride et al. 2004, Vasiliauskas et al. 2004), and are often succeeded by shade-tolerant conifers such as black spruce or balsam fir. Given the general trend of replacement of shade-intolerant by shade-tolerant species and limited dispersal distance in

the forest interior, succession trajectories of conifer and broadleaf forests may appear relatively predictable, resulting in low expert knowledge uncertainty. Uncertainty in published knowledge is low for both conifer and broadleaf forest cover types due to an abundance of literature. More published knowledge is available on natural succession of broadleaf forests and post-fire establishment of coniferous forests (Table 6). Due to differences in shade-tolerance between broadleaf and conifer species, conifer forests may on average become older than broadleaf forests (Hicke et al. 2007) with an increased probability of being destroyed by wildfire. Moreover, the stand structure of conifer forests (e.g., ladder fuels) makes them more likely to be subject to intense wildfires compared to broadleaf forests (Hély et al. 2000). Together this may lead to more frequent observations and published studies of re-establishment following wildfire in coniferous stands.

Expert knowledge uncertainty is higher for mixed forest cover types than for coniferous and broadleaf forest cover types. By definition, mixed forest cover types are a broad group that is relatively species-rich and highly diverse. Mixed forests can originate directly from simultaneous establishment of coniferous and broadleaf species after fire, can form a short phase in the successional transition from shade-intolerant broadleaf to shade-tolerant conifer forests, or may even result from canopy break-up of old conifer forests caused by insect pests, with shade-intolerant broadleaf species re-establishing in larger canopy gaps (e.g., Bergeron 2000). Given the large variation in species composition and mode of origin, mixed forests may follow many different succession trajectories. Moreover, unless exact information about species composition and specific disturbance history is available, it may be difficult to predict the successional course that a particular mixed forest may take, increasing the uncertainty in expert knowledge. There is a dearth of published knowledge about succession of mixed forest cover types compared to that for coniferous and broadleaf forest cover types, for all phases of succession (Table 6). The reasons for this scarcity may be that mixed forests can be short-lived transitional phases between broadleaf and coniferous forest cover types and the opportunity to observe mixed forests may therefore be limited or differences may exist in how mixed forest cover types are classified among researchers.

Overall, knowledge uncertainty for conifer and broadleaf forests is relatively lower than for mixed forest cover types for both expert and published knowledge. However, since published knowledge is less abundant for natural succession in coniferous forests and for post-fire establishment in broadleaf forests, expert opinion may remain an important knowledge source for these processes. Knowledge uncertainty for successional dynamics in mixed forests was found to be high for both expert and published knowledge sources, though mixed forest cover types are considered an important part of boreal forest landscapes, both in Ontario (Towill et al. 2004) and elsewhere (e.g., Cumming et al. 2000, Park et al. 2005). Therefore, we identify mixed forest succession dynamics as a critical knowledge gap and recommend that research efforts focus on this topic. We also recommend that extra attention is needed during applications of the presently uncertain knowledge of mixed forest succession dynamics.

Site conditions

Expert knowledge uncertainty about succession under extreme site conditions (e.g., xeric and poor) is relatively low. This may be because suitability of such sites for establishment and growth of many species is limited and that successional trajectories of forests under extreme site conditions may be more predictable (e.g., Bergeron and Dubuc 1989). Published knowledge of successional dynamics under extreme site conditions is less abundant (Figure 7), with higher uncertainty. This may be due to the relative rarity of some extreme site conditions as well as low interest in sites that are deemed unproductive. As well, little indication of on-going research on extreme sites was found during our survey of researchers.

Uncertainty of expert knowledge was higher for succession dynamics under moderate site conditions compared to extreme site conditions. This may be because moderate site conditions, such as those on mesic and mesotrophic sites, are suitable for establishment and growth of most boreal species, and the species composition on such sites may vary greatly, with many possible successional trajectories. Published

knowledge of succession was relatively abundant on moderate sites (Figure 7), with lower uncertainty compared to extreme sites. This may be simply due to higher availability of moderate sites for research studies, as well as the economic importance of such sites in forest management.

We recommend that research be undertaken investigating boreal forest cover change under extreme site conditions. We consider that it is possible to treat both expert knowledge and published knowledge as hypotheses and formulate models of forest succession for moderate and extreme site conditions, which can be tested against empirical observations of forest cover changes to evaluate the level of local accuracy of the current knowledge.

Spatial context

Expert knowledge of boreal forest succession is largely based on experts' personal observations of short-term dynamics of individual forest stands. Since experts typically have long periods of practical experience, their stand-level observations are abundant and their uncertainty about short-term successional dynamics of familiar forest stands may be expected to be relatively low. Published information about successional dynamics at the stand-level is also abundant and knowledge uncertainty may be expected to be relatively low. In contrast, large scale landscape-level processes that influence forest landscape succession (e.g., Foster et al. 1998) usually exceed the spatiotemporal scale of personal experience by experts, making them difficult to observe. Consequently, stand-level expert knowledge, when re-scaled to landscape level, may differ from observed landscape-level forest cover type changes. Therefore we argue that uncertainty in expert opinion about boreal forest succession is likely to be higher at landscape level.

Landscape-level processes are not the same as stand-level processes multiplied by the surface area covered by the various forest cover types. This multiplication approach is commonplace in forest management, but is too simplistic and does not acknowledge the emergent properties of complex, large-scale systems. We deem that research approaches are needed to address stand-level succession dynamics within their broader, spatial landscape- and regional-level contexts, as well as to extrapolate and scale up the currently rich knowledge of stand-level processes to these levels, to which forest management activities are increasingly migrating. Our recommendations are congruent with recommendations and suggestions made by others: for example, close to three decades ago Heinselman (1973) called for studies into large-scale forest landscape processes that may not be readily inferred from small-scale studies. More recently, Greene et al. (1999) and Schwartz et al. (2003) suggested an integration of neighbourhood effects, such as seed dispersal, into landscape-scale models of forest dynamics, while Woods (2007) emphasized that observations of forest dynamics are scale-dependent and therefore sensitive to scaling operations. Other authors (e.g., Boucher et al. 2006, Bergen and Dronova 2007) have also emphasized the need to understand how landscape-scale dynamics are affected by stand-level factors such as local disturbance history.

In the context of landscape and regional-level processes, long-term forests dynamics are important. Though forest dynamics can be studied over a long period (e.g., Bergeron 2000), most studies are not long term, even when they address landscape-scale processes. The need for research efforts on long-term forest dynamics at the stand- and landscape-level is identified by others as well: for example, Woods (2007) asserted that long-term observations of forest dynamics are essential for addressing questions about late-successional dynamics and Kellomäki (2000) identified the long-term effects of management on forest ecosystem dynamics as a knowledge gap that needs to be addressed to enable accurate long-term forecasts of future forests landscape states.

Uncertainty of published knowledge also appears to be higher at the landscape-level than at the stand level. This is because most published reports have focused on studying and describing forest succession at the stand-level. The few published studies that have been aimed at the landscape-level are not usually

spatially explicit and do not reveal the underlying dynamics that give rise to observed changes in average landscape characteristics (e.g., Gauthier et al. 2000). Consequently, uncertainty in published knowledge about landscape-level boreal forest succession may be relatively high. This assertion is supported by the results of our succession network testing study, which indicate that stand-level published knowledge, when re-scaled to landscape-level, differed from empirical observations of forest succession at landscape-level. However, the re-scaled published knowledge was more similar to empirical observations at landscape-level than the re-scaled expert knowledge.

Overall, the relative level of uncertainty in knowledge about forest succession at the landscape-level is higher for both knowledge sources and we identify this as a knowledge gap.

Precision and accuracy of knowledge

Both sources of knowledge of boreal succession may be viewed by their relative precision and accuracy at landscape level (Figure 14). By precision, we mean the degree of specificity of knowledge, and by accuracy the degree of conformity of knowledge about a phenomenon to its actual state. Our approach of deriving knowledge by integrating published studies renders this knowledge more universally applicable to landscape-level boreal succession in all ecogeographic regions. However, this generality occurs at the cost of ecogeographical precision. Expert knowledge, conversely, is ecogeographically specific and therefore relatively more precise for landscape-level boreal succession with respect to ecogeographical regions. The results of knowledge testing indicate that, overall, expert knowledge did not compare well to empirically observed forest cover change, and did not describe the ecogeographical *differences* in boreal succession that it proposes. Published knowledge compared relatively better to empirically observed forest cover change, and did describe *similarities* in boreal forest succession among study regions. Thus, we deem that, when generalized to landscape-level, published knowledge was more accurate than expert knowledge.

We argue that the balance between precision and accuracy of the two knowledge sources of forest succession have consequences for their utility. The expert knowledge with its strength in precision and details, may be suitable for the description of past and present states of forest stands, as well as stand-

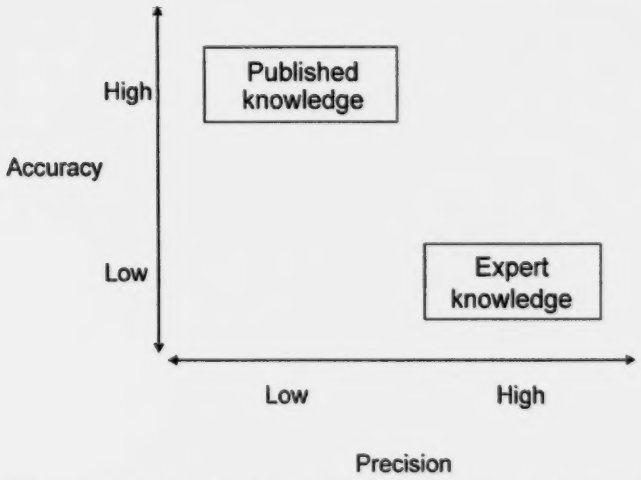


Figure 14. *A hypothesis of expert and published knowledge of landscape-level boreal forest succession, ranked by relative precision and accuracy. (Note: Both axes are categorically scaled into classes, but this does not imply that class width is the same between or within axes.)*

level forecasts under a specific set of local environmental conditions. In contrast, the strength of knowledge from published studies lies in the generalized view of the entire set of possible stand dynamics summarized over a range of conditions, such as geoclimate, neighbourhood effects, and disturbance histories. This may be more suitable for the extrapolation of stand-level knowledge to the landscape-level and for forecasting future forest landscape states.

Furthermore, we assert that low uncertainty does not necessarily mean high accuracy. Despite low uncertainty of expert and published knowledge for successional dynamics of conifer and broadleaf forests at the stand-level (Figure 13), the evidence does not suggest that either knowledge source was highly accurate. Only by testing appropriately scaled expert and/or published knowledge against additional empirical observations of boreal forest dynamics can statements be made about knowledge accuracy.

Synthesis

Knowledge of forest succession has long been key information for developing forest management tactical plans. Increasingly so, forest succession knowledge also is being used at broader scales (for example, at regional level), with quantitative models (e.g., decision support systems), for a variety of goals (for example, state of future forests), and under various assumptions (for example, what-if scenario simulations). As such, reliable forest succession information will be a critical requirement for developing and implementing forest policies and strategic forest management planning – both at broader scales than in the past. It is in this context that we examined the nature of the body of knowledge of forest succession in boreal Ontario.

We remind the reader that our study was exploratory and must not be considered conclusive. Above all, this study and its findings are meant to be a precursor for future studies. The many contraints – conceptual, informational, and resource – necessitated study assumptions, which is an essential methodological context to keep in mind.

Our analyses of boreal forest succession knowledge, from an Ontario perspective, included a logical sequence of steps (Figure 15) where we:

(a) Elicited and summarized expert and published knowledge
(b) Estimated the degree of uncertainty in both sources of knowledge
(c) Examined the level of congruence between the two knowledge sources
(d) Derived explicit and quantitative hypotheses of boreal forest succession from both knowledge sources and tested those against empirical data, and
(e) Identified priority research areas based on the gaps and degree of uncertainty in the knowledge

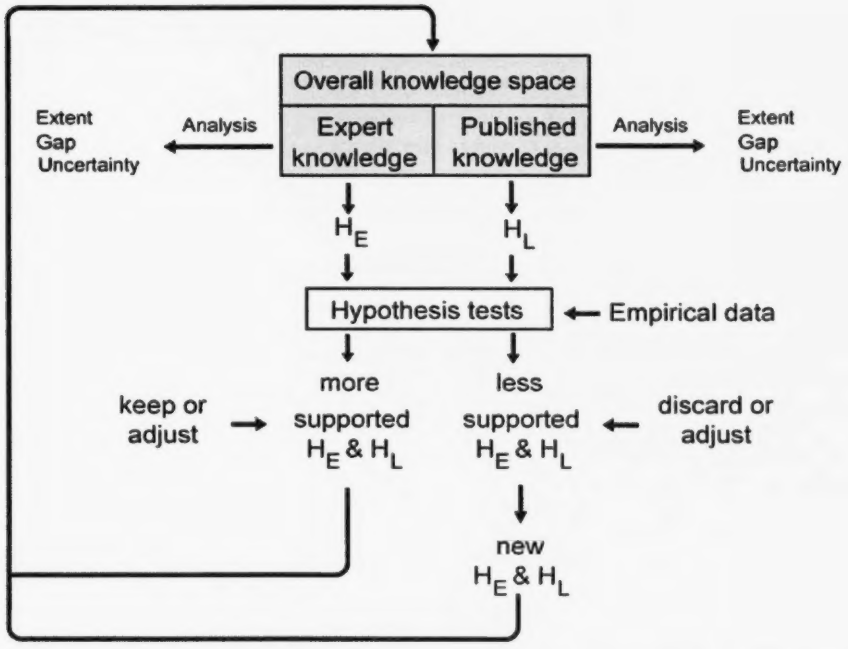


Figure 15. *An illustration of the process used to improve the knowledge of boreal forest succession through methodical inquiry. Iterations of the sequence progressively unify the knowledge and decrease gaps and uncertainty.*

While individual components of this knowledge from both sources may have been examined in the past, little is known about boreal forest succession knowledge in a holistic sense. Through the above process, we characterized the hitherto unknown space of forest succession knowledge to provide a synoptic view from many dimensions. For example, different aspects of boreal forest succession can be positioned along the dimension of degree of uncertainty as illustrated in Figure 16. In sum, by making the latent expert knowledge explicit, merging it with published knowledge, and examining the degree of uncertainty in both knowledge sources, we unveiled the overall properties of forest succession knowledge, and educed the "known knowns" and "known unknowns."

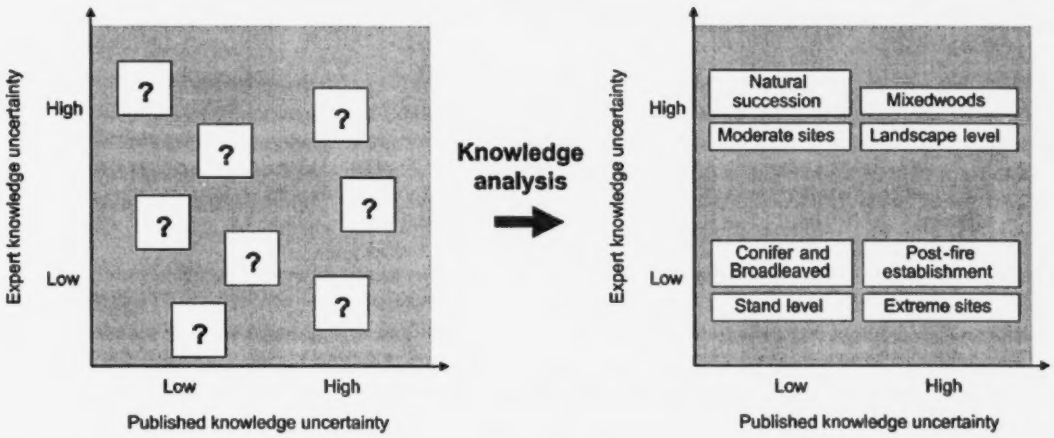


Figure 16. *The relative degree of uncertainty associated with both sources of knowledge on different aspects of forest succession was elucidated by our analysis of the knowledge space.*

This view of the knowledge space in the short term better informs policymakers and forest management planners; they can build the knowledge uncertainty into their applications, and by knowing the relative degree of reliability of different sources of succession knowledge, they can select optimum combinations of expert and published knowledge for specific applications. As well, it identifies the gaps and weaknesses in knowledge that provide specific research foci for individual researchers as well as for agencies that set strategic directions for and fund future research. We identify several focal areas, not necessarily mutually exclusive, for future research on boreal forest succession, as relevant to Ontario.

- *Post-fire establishment and early stand dynamics:* Present knowledge about post-fire establishment, which is a rapid and complex process, is composed primarily of qualitative expert knowledge with few rigorous quantitative studies. This knowledge is key because it provides the foundation for all subsequent succession steps. Elucidating how boreal forest succession progresses following stand-replacing fires will increase the accuracy of disturbance simulation model forecasts.
- *Non-stand replacing disturbances:* Non-stand replacing disturbances such as insect outbreaks are common throughout the boreal forest biome and modify successional trends. Quantitative knowledge about effects of these disturbances is sparse and further research would improve forecasts of succession trajectories, especially for late-successional forests.
- *Natural succession and structural dynamics:* Present knowledge of natural succession is rich but mostly descriptive, which limits its applications in quantitative models. Formulating this body of knowledge as quantitative hypotheses and rigorously testing those will help to improve the quality of that knowledge and advance its use in predictive models.

- *Succession under different site conditions:* Under moderate site conditions, where environmental control of succession processes is weak, expert knowledge of succession is relatively uncertain, and published knowledge is abundant but fragmented. The main need here is to unify and synthesize the extant knowledge. In contrast, under extreme site conditions, succession processes are relatively simple due to strong environmental control. Here, expert knowledge is less uncertain but published knowledge is scarce. Expert knowledge could be used as hypotheses in future research to improve its rigour.
- *Succession in mixed forest cover types:* In contrast to coniferous or broadleaf, mixed forest cover types are variable by definition and exhibit complex successional dynamics, which leads to high knowledge uncertainty in both sources. Given the large extent of mixedwood forests managed in boreal Ontario, improving the certainty of succession knowledge associated with mixed forest cover types is a logical priority.
- *Succession at landscape-scale*: At landscape-scale, knowledge of succession is uncertain for both expert and published sources of knowledge. We consider that increased research effort is needed to broaden the scale of knowledge (to regional-level and long-term) from the present focus on stand-level to meet the scale of policy development and strategic planning. In the long term, this would lead to a coherent and unified body of knowledge, from which the weaknesses can be progressively eliminated, thereby creating a reliable and more accurate knowledge space for various applications.

In summary, we recognized the dichotomy in the body of boreal forest succession knowledge: (a) the published research information on boreal forest succession, and (b) the implicit integration of experience, published knowledge, and informal deductions of forest practitioner knowledge. As well, we noted two other trends: (a) expert knowledge is the primary choice for use in Ontario and (b) published research efforts seldom acknowledged expert knowledge, and rarely viewed forest succession research with a hypothetico-deductive approach.

Our overall recommendations are to (a) recognize and account for the relative uncertainties associated with succession knowledge during its applications, (b) focus future research efforts on the gaps and weaknesses highlighted here, (c) continue to advance the knowledge in a progressive manner with hypotheses testing, and thereby (d) develop a unified body of knowledge, and (e) adopt a formal approach to integrate and utilize expert knowledge in applications as well as to develop testable hypotheses.

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Appendix 2.

Details on linking population dynamics and age class distribution. Age class distributions can be employed to estimate forest age classes relevant to natural succession by using methods from life table analysis.

Age class distributions were calculated for the extracted data described in the *Nature of published knowledge* section and analyzed by applying basic concepts from population dynamics, such as renewal rate, mortality rate, and survivorship. Applied to this study, the renewal rate of forest cover type *i* is the rate at which stands of this forest cover type are emerging on the landscape, while its mortality rate is the rate at which these stands are disappearing from the landscape. We assumed that the population of natural origin forest stands of forest cover type *i* in boreal North America is stationary relative to the scale of our study. This means that for each forest cover type *i* (i) the number of stands, (ii) the stand renewal rate, and (iii) the stand mortality rate are all constant. Accepting this assumption, we can analyze an age class distribution of forest stands using life table methods and derive hypotheses about timing of succession as outlined below.

Based on Lotka (1907) and modified by Cole (1954), the age class distribution and age-specific survivorship of a population are linked by the relationship

$$c_{x_i} = \frac{e^{-r_i x_i} l_{x_i}}{\sum_{x_i} e^{-r_i x_i} l_{x_i}} \qquad \text{(A1)}$$

Here, x_i is a stand age class of forest cover type *i*, c_{x_i} is the relative frequency of stands in age class x_i, r_i is the relative population growth rate of forest cover type *i*, and l_{x_i} is the relative survivorship from age classes 0_i to x_i. Since we assumed that the number of forest stands is constant, we can set $r_i = 0$ reducing (A1) to

$$c_{x_i} = \frac{l_{x_i}}{\sum_{x_i} l_{x_i}} \qquad \text{(A2)}$$

In a standard life table, the relative survivorship l_{x_i} can be calculated as

$$l_{x_i} = \frac{n_{x_i}}{n_{0_i}} \qquad \text{(A3)}$$

Here, n_{0_i} and n_{x_i} are the numbers of stands in age classes 0_i and x_i, respectively. Substituting (A3) in (A2), we write

$$c_{x_i} = \frac{n_{x_i}}{\sum_{x_i} n_{x_i}} \qquad \text{(A4)}$$

Since c_{x_i} is defined as the relative frequency of stands in age class x_i, equation (A4) is true by definition, thus illustrating the relationship between age class distribution and relative survivorship.

Based on age class distributions we constructed a life table for each forest cover type *i*. The age class distribution of most forest cover types shows a peak for intermediate age classes, which we interpreted as indicating the transition from an initial phase of succession to forest cover type *i* for younger stands ($\sum p_i = 0$) to the subsequent phase of succession away from forest cover type *i* ($\sum p_i > 0$) for older stands. Since we are interested in succession leading away from forest cover type *i*, we used this peak in age class distributions as age class zero and concentrated our analyses on the subsequent age classes.

We constructed life tables following the approach of Caughley (2004). We fitted a logit model to the relative frequency distribution of age classes and

back-transformed the fitted model to an absolute frequency distribution of age classes. Using the fitted, absolute age-class distribution, we calculated the relative survival rate from age classes x_i to x_i + 1 $\left(s_{x_i} = n_{x_i} / n_{x_i+1}\right)$, which is a standard life table variable. The probability of succession of a stand in age class x_i, p_{ijx_i}, is equivalent to the relative survival rate for the previous age class, i.e., from age classes x_i - 1 to x_i, s_{x_i-1}.

We used the relative survival rate, s_{x_i}, for deriving hypotheses about forest ages that are important in the context of forest succession:

We interpreted the lowest age class for which $s_{x_i-1} < 1$ as the age at start of succession, t_{start_i}. This age class is our published knowledge hypothesis about age at the start of succession from forest cover type *i* to any *j*.

We interpreted the age class for which $s_{x_i-1} = s_{x_i-1,\max}$ as the age with maximum probability of succession, $t_{\max_i}$. This age class is our published knowledge hypothesis about the age at maximum probability of succession from forest cover type *i* to *j*, summed over all *j*.

Since s_{x_i} approaches zero asymptotically, it is not easy to interpret this variable for finding the age at the end of succession, t_{all_i}, and we did not derive a published knowledge hypothesis for this age.

Appendix 3.

Details on measures used to quantify similarity between expert and published succession networks and between expert and published estimates of forest ages.

The index of edge similarity for networks, *S(L,E)*, makes use of the principle of the Hamming distance (Hamming 1950) that quantifies the difference between two sets of symbols:

$$S(L,E) = 1 - \left(\frac{1}{\Delta E_{\max}} \sum_j \left| L_j - E_j \right| \right) \quad \text{(A5)}$$

Here, *L* and *E* are the published and expert succession networks and L_{ij} and E_{ij} are the elements of their matrices, while ΔLE_{max} is the maximum possible difference between the two matrices. The value of ΔLE_{max} is found by heuristically re-arranging the elements of the two matrices such that the summed difference over all re-arranged elements is at maximum. Division by the maximum possible difference standardizes the Hamming distance; where one indicates maximum similarity of networks and zero indicates the minimum. Increasing *S(L,E)* indicates increasing similarity between networks.

Pearson's product-moment correlation, *cor(L,E)* for two networks (Butts and Carley 2005) uses the adjacency matrices of the succession networks:

$$cor(L,E) = \frac{\mathrm{cov}(L,E)}{\sqrt{\mathrm{cov}(L,L)\mathrm{cov}(E,E)}} \quad \text{(A6)}$$

$$\mathrm{cov}(L,E) = \frac{1}{N^2 - 1} \sum_j \left(A_j^L - \mu_L \right)\left(A_j^E - \mu_E \right) \quad \text{(A7)}$$

Here, *N* is the set of forest cover types, while A_j^L and A_j^E are the adjacency matrices of the networks *L* and *E* and μ_L and μ_E are their means. Pearson's product-moment correlation varies from -1 to +1. Increasing *cor(L,E)* indicates increasing similarity between networks.

Similarity between published and expert estimates of forest age at start of succession is quantified as the relative similarity between stand ages, $T_i(L,E)$, by dividing the absolute age difference by the mean:

$$T_i(L,E) = 1 - \frac{\left| t_{L,start_i} - t_{E,start_i} \right|}{\frac{1}{2}\left(t_{L,start_i} + t_{E,start_i} \right)} \quad \text{(A8)}$$

Where $t_{L,start_i}$ and $t_{E,start_i}$ are forest ages at start of succession from published and experts. Increasing $T_i(L,E)$ indicates increasing similarity between age estimates.

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(0.3k P.R., 08 12 30)
ISBN 978-1-4249-7871-7 (print)
ISBN 978-1-4249-7872-4 (pdf)